SEED AND VEGETATION DYNAMICS IN UNDAMAGED AND DEGRADED COASTAL HABITATS OF THE HUDSON BAY LOWLANDS

by

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A thesis submitted in conformity with the requirements for the Degree of Master of Science, Graduate Department of Botany, University of Toronto

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Abstract

Grubbing and grazing by increasing numbers of lesser snow geese (*Anser caerulescens caerulescens*) have led to loss of vegetation and soil degradation in salt marshes and on beach ridges. These changes have had a deleterious effect on the soil seed bank by reducing density of seeds and shifting the composition from species present prior to the disturbance to invasive species. In the salt marsh, more recently degraded plots had greater revegetation potential from the remaining seed bank than plots where loss of vegetation was of long standing. Seed banks in beach-ridge soils were less affected by degradation due to the greater proportion of weedy species present in the original vegetation. Studies of the seed and vegetation dynamics in the supratidal marsh indicated that while there were no systematic differences between the seed rain in undamaged and degraded sites, degradation processes constrain recruitment at the entrapment, germination and establishment stages.

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Chapter One: Introduction

1.1 Opening Statement

Modes of regeneration and growth of plants can be organized according to generalized groups of morphological, physiological or phenological traits that vary predictably along environmental gradients and influence species-richness in plant communities (Grubb 1977). These modes of regeneration are termed "strategies" (*sensu* Grime 1977, Shipley *et al.* 1989). In a review of life-history strategies, Southwood (1988) recognized three gradients that shape the species composition of communities: axes of disturbance and adversity, and a biotic interactions axis that is predicted to increase as the intensity of the first two axes decreases. Disturbance is associated with the partial or total destruction of the plant biomass and the adversity or stress axis refers to conditions that restrict biomass production (Grime 1977).

In Grime's classification (1979), where the strategies of adult and juveniles stages of plants are separated, the responses of mature plants to environmental and biotic gradients correspond approximately to ruderal, stress-tolerator and competitor strategies respectively. Ruderals are favoured during conditions of low stress and high disturbance, stress-tolerators are selected when conditions of high stress and low disturbance prevail and competitors dominate the vegetation when both stress and disturbance are low. These three strategies are thought to represent evolutionary extremes and the life-history strategies of most plant species represent compromises between conflicting selection pressures. It is important to note that no viable strategies are predicted for habitats where both stress and disturbance are high.

Grime (1979) identified five methods of regeneration: spread through vegetative (clonal) expansion, seasonal regeneration of vegetation gaps through transient seed banks, persistent seed banks, production of numerous wind-dispersed seeds and persistent long-lived seedlings. As juvenile stages can rarely exert competitive pressure on established plants, these five methods of regeneration are linked to strategies involving escape from suppression by established vegetation in time or space (persistent seed bank, wide-spread dispersal and seasonal regeneration) and toleration of stress through physiological means (vegetative expansion, persistent seed banks and persistent seedlings) (Shipley *et al.* 1989). Trade-offs in life-history traits have been predicted between adult longevity and the seed regeneration capacity of species over time (seed bank) and space (seed dispersal) and these are summarized in Figure 1 and Table 1 (van Groenendael *et al.* 1998).

Table 1. Three hypothetical combinations of life-cycle traits represented by groups A to C. Each combination represents one corner of the triangular diagram of Fig. 1, by reading this diagram counter-clockwise. As the value of one of three traits is determined by the way the diagram is read, these values are placed between brackets (modified from van Groenendael *et al.* 1998)

Trait	A	B	C
Seed longevity	Long >5 years	Short <5 years	(Short <5 years)
Adult (genet) longevity	(Short <5 years)	Long >5 years	Short <5 years
Distance of dispersal	Close to adult	(Close to adult)	Far from adult
Breeding system	Selfing	Outcrossing (wind)	Outcrossing (insect)

There may be more than one viable evolutionary response to an environmental challenge (Southwood 1988). Ellner (1987) explored two alternative strategies to randomly varying environments that he called "high risk" and "low risk." These two

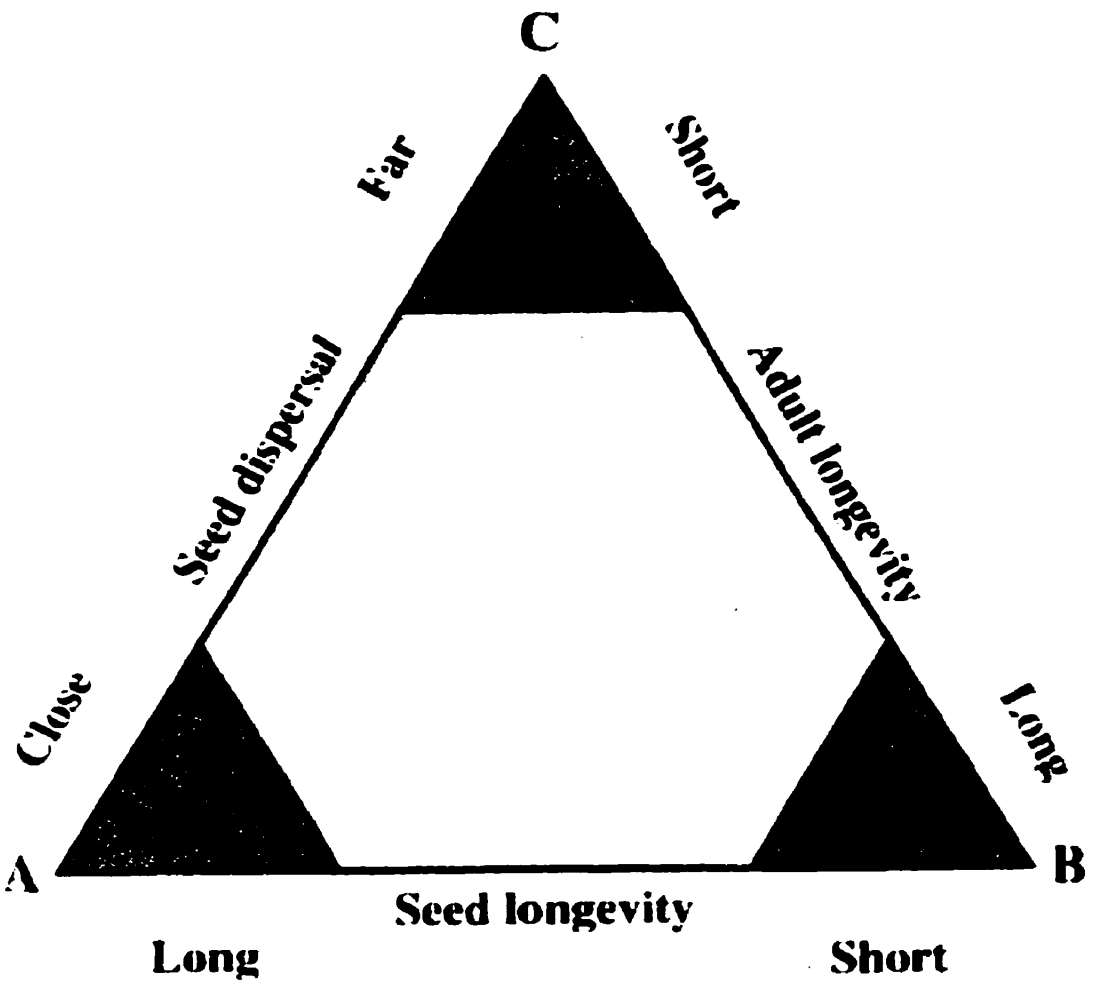


Figure 1. Hypothetical trade-offs between seed longevity, dispersal capacity and adult longevity. Letters refer to combinations of life-cycle traits as presented in Table 1. Modified from van Groenendael *et al.* (1998).

strategies are very similar to an independent classification of "spenders" and "savers" based on studies of chalk grassland forbs in the Netherlands (reviewed by During *et al.* 1985). In these classifications, environmental variability is characterized by an intermittent, unpredictable stress or disturbance that reduces the performance of all species. "High risk" and "spender" strategists gamble on future conditions being favourable and reap large benefits when such scenarios occur. "Low risk" and "saver" species employ an alternate, more cautious strategy where they are better equipped to tolerate stress but are inferior in performance to "high risk" and "spender" species when conditions are favourable for plant growth. Alternate strategies allow for co-existence of species under similar disturbance and stress regimes.

The regeneration strategies of plants in communities are shaped by patterns of disturbance and stress they have been subjected to in the past, which act as selection forces over evolutionary time. Human dominion of the earth's ecosystems has instigated changes of the processes associated with these gradients on very large scales and at greatly accelerated rates (Vitousek *et al.* 1997). The ability of natural regeneration processes of plants to restore degraded areas, brought about by anthropogenic intervention, is not well documented and the accelerated rates of change appear to exceed the capacity of the regeneration processes to cope.

1.2 Formation of soil seed banks in relation to gradients of disturbance and stress

Thompson (1978) asserted that two broad theoretical considerations are significant in discussion of the density and distribution of soil seed banks: gradients of disturbance and gradients of stress. When disturbance is severe and frequent, plants are expected to invest a high proportion of their resources in reproductive effort in order to survive the

disturbance. Seeds buried in the soil provide a source of regeneration *in situ*, which may confer an advantage following a disturbance event. However, the maintenance of high densities of buried seeds can be quite costly as seeds have high mortality from a variety of causes (Rees 1997). As a consequence, the formation of large soil seed banks is a viable strategy only when selection for buried seeds is very strong, due to high rates of disturbance or when production is sufficient to support a high reproductive effort, as occurs under low stress conditions. In summary, the density of buried viable seeds is predicted to be positively correlated with disturbance and negatively correlated with stress (*sensu* Grime 1977).

These two gradients are often negatively correlated with each other. However, as mentioned above, difficulties arise when disturbance intensity and frequency increase in tandem with increments of stress on plants as no viable plant strategy is possible when both disturbance and stress are high. When in a dormant state, some seeds may survive for longer periods under regimes of high stress and high disturbance than their adult counterparts. In a review on the practical use of dispersules in restoration, Strykstra *et al.* (1998) pointed out that the initial seed population becomes gradually depleted, as seeds succumb to unsuccessful germination, predation, decay or aging, after the extinction of a plant population. Asymptotic models can be used to model seed bank decline but it is difficult to predict survival chances for the tail of the distribution, which represents those seeds that survive the longest, as factors influencing survival in earlier periods may be different from those influencing later periods. Density of the seeds stored in the soil is strongly influenced by the time elapsed since the onset of unfavourable circumstances (Bekker *et al.* 1997), the potential longevity of the seeds which is determined by

physiology, and the effects of environmental and biotic factors on the preservation and retention of the seeds. Species-specific traits related to potential longevity of seeds include type of seed dormancy, structure of seed coat, defence compounds (Hendry *et al.* 1994), amount and type of seed reserves, and efficiency of basic metabolism (Hendry 1993) (as reviewed by Bekker 1998). Environmental factors shown to affect survival in the soil include nutrient status, oxygen availability, moisture, temperature fluctuations and pH (Villiers 1972, Baskin & Baskin 1989, Karssen & Hilhorst 1992). For example, soil moisture was shown to differentially affect the survival of seeds depending upon whether the species were usually found in wet or dry grasslands (Bekker *et al.* 1998a).

Opportunities to directly estimate the longevity of seeds found in naturally buried populations arise only under certain circumstances. These include instances where 1) the last time a species grew on a site can be ascertained with moderate accuracy, such as weed seeds buried under formerly arable lands and shade-intolerant species buried under woodlands or plantations of known age, 2) seeds were buried beneath volcanic ash (Whittaker *et al.* 1995) or buildings of known age (Odum 1965) and 3) where fresh seed input was inhibited through close-cutting or the use of herbicides (as reviewed by Bakker *et al.* 1996a and Baskin & Baskin 1998). Burial experiments have been used to estimate seed longevity of different species but their results must be interpreted with caution as they bypass natural burial mechanisms and are therefore vulnerable to overestimation errors (Bakker *et al.* 1996a).

In many cases, indirect sources of evidence, such as burial depth, must be used to estimate longevity. The abundant evidence that more deeply buried seeds tend to be older than seeds in shallow depths allows the ratio of the deeply buried seeds to seeds

found in shallow depths to be used as an index of longevity (Thompson *et al.* 1997, Bekker *et al.* 1998b). However, discrepancies can occur (Poschlod 1993, as reviewed in Thompson *et al.* 1997), perhaps partly due to the activities of earthworms (Willems & Huijsmans 1994). Thompson *et al.* (1997) developed a dichotomous key to classify seed bank types (transient, short-term persistent, long-term persistent) using both direct and indirect evidence (Fig. 2) that includes seed depth.

1.2.1 What is the effect of disturbance on the soil seed bank?

Tests of predictions of the density of buried seeds along disturbance gradients have yielded generally negative results. Highly disturbed sites were found to have greater densities of buried seed in high Arctic sites on Ellesmere Island than those in less disturbed sites (Freedman *et al.* 1982). Very large soil seed banks were found in some disturbed coastal sub-Arctic ecosystems on Hudson Bay (Staniforth *et al.* 1998) but comparisons were not made with comparable undisturbed sites. In contrast, increased grazing intensity (Kinucan & Smeins 1992, Ungar & Woodell 1996, Jutila 1998), increased intensity of cryoturbation (Ebersole 1989), the incidence of fire and drawdown in a marsh (Smith & Kadlec 1985), experimental increase in number of disturbance factors (Ingersoll & Wilson 1990), human disturbance (Wisheu & Keddy 1991) and various disturbance regimes (Fox 1983, Pierce & Cowling 1991, Chambers 1993, McGee & Feller 1993) all failed to result in an increase in the density of seeds stored in the soil.

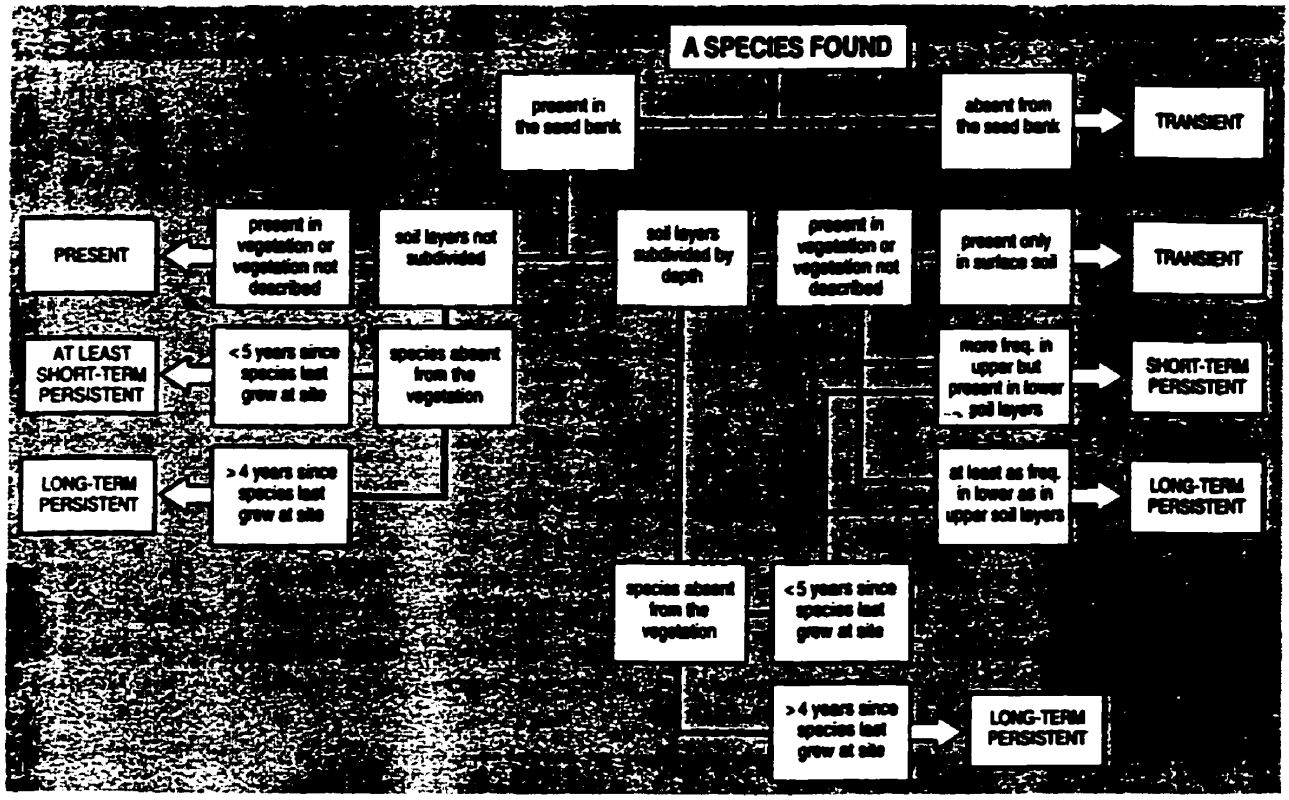


Figure 2. A dichotomous key to three seed bank types determined by using direct evidence and depth distribution; transient (<1 year), short-term persistent (<5 years) and long-term persistent (>5 years). Modified from Thompson *et al.* (1997).

The relationship between disturbance and density of accumulated seeds is a complex one and can be influenced by a number of factors, that both directly and indirectly involve the life-history strategies of plants. Disturbance regimes can affect the relative abundance of seeds in the seed bank of different species with different life-history strategies. In salt-marsh communities in South Wales, the soil seed banks of sites heavily grazed by sheep only consisted of two annuals (Ungar & Woodell 1996). Sites subjected to heavy, continuous grazing in a semi-arid grassland in Texas had a high proportion of early-seral, dicotyledonous annuals in the seed bank, while ungrazed sites had a high proportion of late-seral, monocotyledonous perennials (Kinucan & Smeins 1992). Generally, early-successional annuals (ruderals) tend to produce greater numbers of seeds than later-successional perennials (Grime 1979) and a shift in species abundance towards the first group is a possible influence on the overall density of buried seeds.

The greatest number of different plant strategies may be evident at intermediate levels of disturbance along an arbitrary scale of increasing disturbance. In Mediterranean pastures subjected to mechanical disturbance (Levassor *et al.* 1990) and grazed salt marshes on the Gower Peninsula in Wales (Ungar & Woodell 1996), sites with apparent intermediate levels of disturbance had the highest species richness, consistent with Connell's intermediate disturbance hypothesis (1978). At high levels of disturbance, the numbers of species contributing to the soil seed bank decreased sharply.

Persistence of seeds has been predicted to be greater in disturbed habitats than in "stable" (undisturbed) habitats. According to bet-hedging models, natural selection should favour species in which only a fraction of its yearly output of seeds germinates immediately in variable habitats (Venable & Brown 1988, Rees 1993) as diversified

germination behaviour spreads out the risk in unpredictable habitats (Haig & Westoby 1988). A study using a recently published database of the soil seed banks of north west Europe (Thompson *et al.* 1997) provided evidence in support of this prediction on a broad geographic scale for north-western Europe, as gradients of habitat disturbance were accompanied by predictable changes in seed persistence (Thompson *et al.* 1998). In some studies, density of seeds is, in part, related to the longevity of seed banks.

The prediction of positive correlation between disturbance and density of buried seeds was formulated using a model of plant strategies in relation to an environmental gradient (Thompson 1978). Life-history strategies of plants are very useful in predicting the properties of soil seed banks in relation to gradients of disturbance, but perhaps Thompson's original hypotheses (1978) oversimplified the relationship. More recent papers published in this decade tend to concentrate on issues of longevity of seeds (Thompson *et al.* 1998), coupling between the existing vegetation and the characteristics of the seed bank (Looney & Gibson 1995, Ungar & Woodell 1996) and seed bank dynamics (Levassor *et al.* 1990, Chambers 1993) in relation to disturbance, including predation and disease, rather than density *per se*.

1.2.2 What is the effect of stress on the soil seed bank?

Southwood (1988) identified Grime's (1977) axis of stress variously with "severity of the environment" (Reichle *et al.* 1975), "habitat (un)favourableness" (Southwood 1988, Greenslade 1983), "productivity" (Hildrew & Townsend 1987), "growth rate" (Sibly & Calow 1985), "abiotic stress" (Welden & Slauson 1986) and "resource level"

(Southwood 1988, Wiggins *et al.* 1980). Numerous sources and types of stress exist but only stress associated with low temperature and high salinity will be considered here as they relate to this particular study.

In his review, Thompson (1978) predicted declines in the density of seeds buried in the soil with increasing latitude (Johnson 1975) and altitude (Milton 1939) due to stress arising from low temperatures and short growing seasons. In a review on arctic and alpine systems, McGraw & Vavrek (1989) did not observe a poleward decrease in the density of soil seed banks in tundra communities. Seven studies (Freedman *et al.* 1982, Fox 1983, Archibold 1984, McGraw 1980, Gartner *et al.* 1983, Roach 1983, Leck 1980) covering 18 sites were reviewed and in some, seed densities comparable to those found in temperate systems were reported. However, Fox (1983) observed an increase in soil seed bank size that was correlated with increases in current-year above-ground biomass. Low temperatures enforce dormancy on seeds stores in the soil. However, cold stratification results in germination of seeds at low temperatures (~5°C) for many Arctic species (Gartner 1983).

A considerable amount of research has been conducted on the effects of salinity on plants by both ecologists and physiologists (Adam 1990, Packham & Willis 1997). Most seeds of halophytes exhibit physiological dormancy (Baskin & Baskin 1998) which can become enforced when seeds are exposed to saline environments (reviewed by Ungar 1978). All vascular species studied display both a delay in germination and reductions in the percentage of germinated seeds as salinity increased beyond the level "optimal" for the species. However, halophytes differ from glycophytes in that they are able to remain dormant under highly saline conditions and recover when the salinity is reduced (Ungar

1978, Woodell 1985, Ungar 1991, Keiffer & Ungar 1997) suggesting that they are inhibited by osmotic stress rather than specific ion toxicity under saline conditions (Ungar 1978).

Although the effects of salinity on plant growth, seed germination (Ungar 1978, Woodell 1985, Keiffer & Ungar 1997) and seedling recruitment (Shumway & Bertness 1992) have been studied, few investigations have considered the effect of salt *per se* on soil seed bank formation and size. The size of seed reserves found in salt marshes has been shown to be extremely variable (700 seeds m^{-2} in Hopkins & Parker 1984; 936 to 15 604 seeds m^{-2} in Ungar & Woodell 1996; 699 to 39 204 seeds m^{-2} in Staniforth *et al.* 1998). Most of the species of seed found in these systems were halophytes. Halophytes can be defined as plants that are able to complete their life cycles in a saline environment (Flowers *et al.* 1986, Adam 1990), that includes flowering and producing seeds (Baskin & Baskin 1998). All plants reach the limits of their tolerance at some salinity and even most halophytes would be inhibited by the extreme levels of soil salinity recorded in the salt marshes of La Pérouse Bay, Manitoba (up to ~120g of solutes per litre in the soil solution, i.e. 4x the salinity of oceanic sea water).

1.3 Vegetation loss and soil degradation processes at La Pérouse Bay in relation to seed bank dynamics

1.3.1 Site and vegetation description

La Pérouse Bay (58°44'N, 94°28'W) is located 32 km east of Churchill, Manitoba, on the coast of the Hudson Bay lowlands. Due to freshwater inflow from rivers, shallow coastal waters have relatively low salinity (c. 4g of dissolved salts l^{-1}) compared to deeper waters

of the Bay (30-33g l^{-1}) (Jefferies *et al.* 1979). Coastal regions of the lowlands derive their salts from underlying fluvio-marine deposits of the postglacial Tyrell Sea in which the pore water salinity is 21-25g l^{-1} (Price & Woo 1988a,b). High tides at the approach of autumnal equinox and meltwater in spring flush the surface sediments of salts in intertidal and supratidal salt marshes (Jefferies *et al.* 1979, Price and Woo 1988b, Iacobelli & Jefferies 1991). Due to impeded drainage and the low salinity of tidal waters, an inverse salinity gradient exists in these coastal marshes with highest soil salinities recorded landward from the coast in the upper levels of the intertidal marsh or in the supratidal marsh beyond the high-water mark of spring tides (Jefferies *et al.* 1979). The supratidal marshes are flooded with tidal water about twice every three years.

Permafrost is continuous in the Churchill region (Rouse *et al.* 1997) and, in these coastal salt marshes, it is found at depths of 25-30cm below the surface in mid-summer (Wilson & Jefferies 1996). The soils of intertidal and supratidal marshes are regosolic static cryosols (Canadian Soil Classification System, Agriculture Canada 1987) characterized by a gley mineral horizon (Cg) and a surface Ah horizon that is very shallow close to the coast (Wilson & Jefferies 1996).

Isostatic uplift, at an estimated rate of 0.5cm to 1.2cm per year (Andrews 1973), exposes coastal flats in the region. The intertidal flats, where undamaged, are covered with a graminoid sward consisting of *Puccinellia phryganodes* and *Carex subspathacea* (Fig. 3: A) (nomenclature follows Cody 1996). Associated dicotyledonous species include *Potentilla egedii*, *Plantago maritima*, *Ranunculus cymbalaria* and *Stellaria humifusa*. As areas become increasingly saline associated with loss of vegetation brought about by goose foraging (see below), *Salicornia borealis* and *Senecio congestus* invade

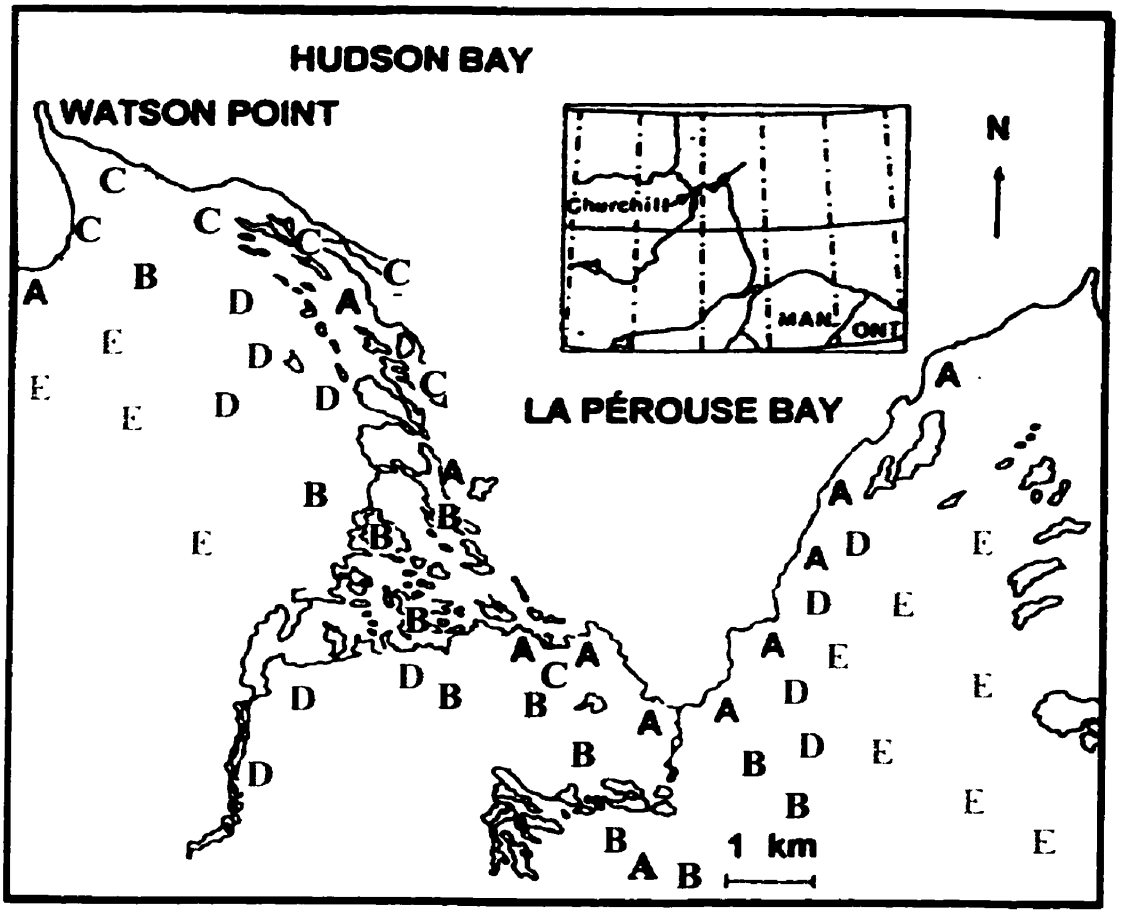


Figure 3. Map of La Pérouse Bay and the coastal zone, the position of which is indicated by an arrow on the Hudson Bay coast on the inset map. A, intertidal or secondary inland salt marshes; B, willow-grassland supratidal marsh; C, beach-ridge vegetation including *Leymus mollis*; D, tall willow species; E, freshwater sedge meadows. Modified with permission from Jano *et al.* (1998).

degraded *Puccinellia-Carex* swards. In the supratidal marsh, grassland (Fig. 3: B) is present on land raised by isostatic uplift and frost-heave action and the vegetation consists of low shrubs, *Salix brachycarpa* and *Salix myrtillifolia*, and two caespitose grasses, *Calamagrostis deschampsioides* and *Festuca rubra*. Even in these marshes, *S. borealis* establishes where there has been a loss of vegetation and erosion of surface organic material. A beach ridge extends along the western coast of the Bay for almost 3km. The extensive stands of *Leymus mollis* that formerly grew on the ridge and associated sand areas have all but disappeared due to intense shoot-pulling by geese (Fig. 3: C). Tall willow (Fig. 3: D) and fresh-water sedge communities (Fig. 3: E) also occur in riparian areas and in freshwater sedge meadows inland from the coast. General descriptions and locations of these communities are given in Jefferies *et al.* (1979) and Jano *et al.* (1998).

1.3.2 Effect of lesser snow geese on the vegetation and on edaphic conditions in coastal marshes

Records show that the mid-continent population of lesser snow geese (*Anser caerulescens caerulescens*) that breeds around the shores of Hudson and James Bays, on Baffin Island and in Queen Maud Gulf (Abraham *et al.* 1996) has been increasing for the last three decades at about 5% to 7% per annum. The mid winter index (not an absolute count) rose from 0.8 million geese in 1969 to 2.7 million in 1995 (Mississippi and Central Flyway Councils, unpublished data). The breeding colony at La Pérouse Bay has been increasing exponentially at the rate of 7% per annum from 1300 breeding pairs in

1968 to 22,500 pairs in 1990 (Cooke *et al.* 1995). In 1994, the population was estimated at 44,500 pairs (Abraham, K.F., Ross, K. & Rockwell, R.F., unpublished aerial survey). The population growth has been linked to nutrient subsidies gained in agricultural areas adjacent to wintering grounds and along migration routes, decreases in hunting pressure and creation of winter refugia (Abraham *et al.* 1996). The increasing numbers of geese have led to substantial changes in the spatial and temporal scales of disturbance associated with foraging by lesser snow geese on the coastal breeding grounds around the Hudson Bay and elsewhere.

The frequencies of many dicotyledonous species of the intertidal and supratidal marshes decline in response to grazing by geese. Removal of geese from salt-marsh vegetation based on exclosures resulted in higher numbers of dicotyledonous species (Bazely & Jefferies 1986). Consumption of apical meristems, stolons and flowers by geese leads to little regrowth or successful reproductive effort in these plants, which are less tolerant of grazing than the main forage graminoid species, *P. phryganodes* and *C. subspathacea*, that possess basal meristems (Sadul 1987).

However, bare patches are generated in graminoid swards as geese grub for roots and rhizomes in early spring before the growth of above-ground vegetation. Continued stripping of turf by increasing numbers of geese leads to destruction of the vegetation through a self-amplifying positive feedback between decreases in biomass and increases in soil salinity (Srivastava & Jefferies 1996). Removal of live vegetation and the insulating layer of litter by geese, accompanied by increased soil surface temperatures and increased rates of evapotranspiration, leads to the upward movement of fossil salts in the soil column and their accumulation at the soil surface. Hypersaline conditions

inimical to plant regeneration result once the layer of vegetation has been removed or dies. Where vegetation has been lost from a site, soil erosion increases substantially. Artificial grubbing in supratidal willow-grasslands led to the death of *Salix* stands within two years (Iacobelli & Jefferies 1991). On nearby beach ridges, loss of soil moisture and organic litter, erosion of soil and exposure of surface mineral layers has accompanied pulling of lyme grass (*Leymus mollis*) shoots by geese. Thus, abiotic stress on plants is linked to biotic disturbances in these systems and these two processes are closely coupled.

The increase in the intensity, periodicity and spatial scale of disturbance by geese, which is linked to changes in edaphic conditions, has triggered the conversion of tracts of salt-marsh vegetation into mud flats, largely devoid of vegetation. Other coastal habitats, such as beach ridges and fresh water sedge meadows, have also suffered similar losses in standing crop and exposure of underlying substrates (Kotanen & Jefferies 1997, Jano *et al.* 1998). The loss of vegetation and soil degradation has been documented at a landscape level in aerial surveys (Kerbes *et al.* 1990, Abraham & Jefferies 1996) and from remote sensing imagery (Jano *et al.* 1998).

1.4 Seed and vegetation dynamics: availability of diaspores vs. "safe sites"

In order to feasibly assess revegetation potential in a system, the processes governing production of dispersal units by vegetation and their recruitment into the vegetation must be documented. In this way, factors that influence processes that, in turn, constrain regeneration processes can be identified.

Seed banks are much more dynamic than they are often portrayed (Chambers & MacMahon 1994). Since the development of quantitative models portraying the formation, persistence and depletion of soil seed banks (Schafer & Chilcote 1969, Roberts 1972), scientists have been gathering data to incorporate into these models (Baskin & Baskin 1998). A graphical representation of a general model of seed bank and vegetation dynamics is given in Figure 4 (modified from Simpson *et al.* 1989). Vegetation is ultimately propagated either through vegetative means or through seed sources. Mechanism of vegetative propagation include those where offspring remain attached to the parent (tillering) and those where plant fragments or special units (vivipary) are able to disperse away from the parent. The seed rain determines seed input, and within communities, this is composed mostly of local production although long-distance dispersal may also be important. The effects of seed predation, which can occur before or after dispersal, has been much studied in relation to phenomena such as seed masting (Silvertown 1980, Waller 1993) and the shapes of seed shadows. The survival of seeds in the seed bank has been linked to probability of burial and the associated probability of escape from predators (Thompson 1987). The effect of granivory on soil seed banks is reviewed by Louda (1989). Other sources of loss from the seed bank include failed germination, physiological death, pathogens, deep burial and redispersal. The effect of fungi and pathogens on soil seed banks (Crist & Friese 1993), and the vertical movement of seeds due to the activities of earthworms (Grace 1984, Willems & Huijsmans 1994), mammals (Gaudet 1977, McGraw 1987), cracks which form during drying (Gunther *et al.* 1984) and percolation (McGraw 1987) have been less

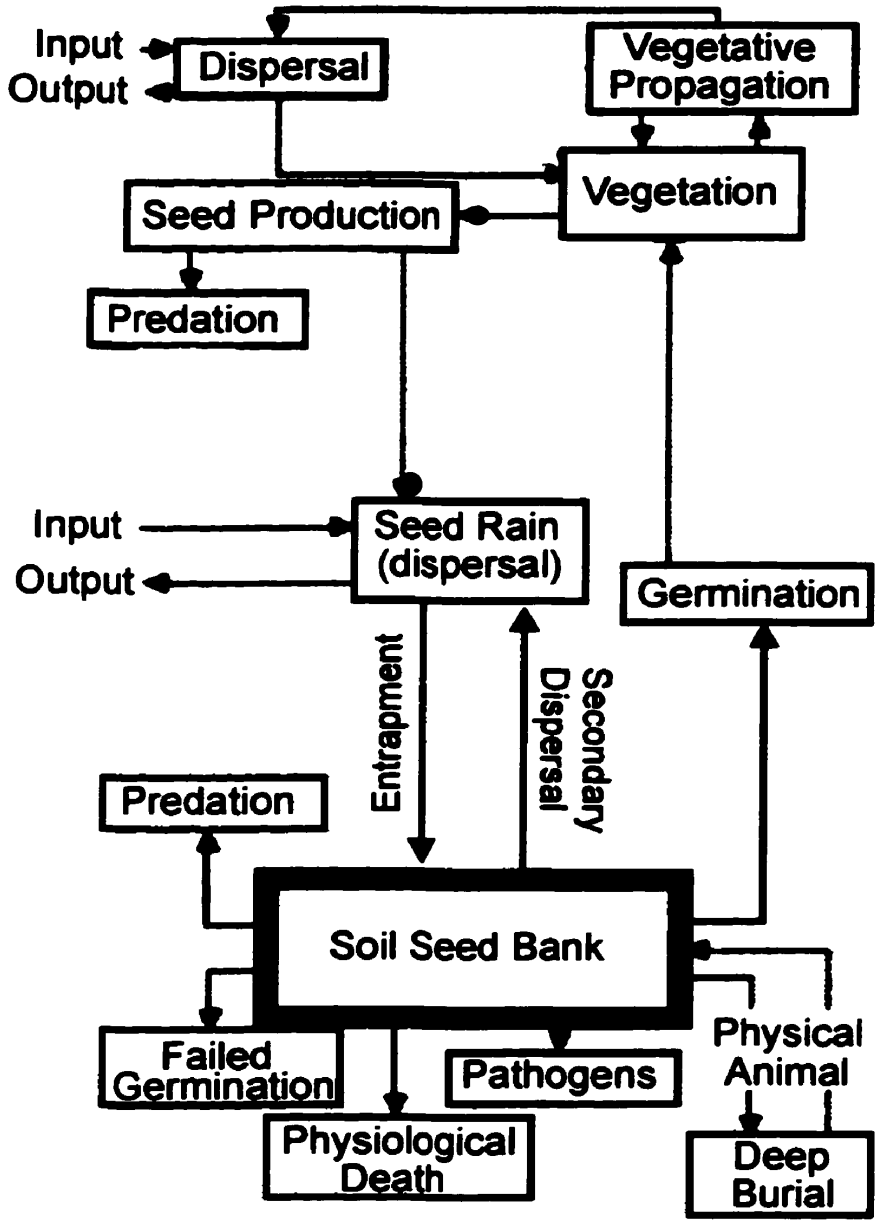


Figure 4. General model of seed bank and vegetation dynamics. Modified from Simpson *et al.* (1989).

studied (McGraw 1987, Leck & Simpson 1987) than other aspects of seed bank dynamics.

Seed bank dynamics are heavily influenced by the movement of seeds through all the stages as shown in Figure 4. Morphological characters such as seed size and shape have been linked to various aspects of seed ecology such as predation risk, dispersability, landing, seedling establishment, burial and persistence (Harper *et al.* 1970, Peart 1984, Thompson 1987, Thompson *et al.* 1993, Bekker *et al.* 1998b). In summary, larger seeds are predicted generally to suffer greater predation risk, to disperse shorter distances, to produce more competitive seedlings, to be less likely buried and to have shorter longevity than smaller seeds.

Every stage shown in the model interacts with biotic and abiotic elements of the habitat where these dispersal and establishment processes are occurring. As Grubb asserted in his description of the "regeneration niche" (1977), the interface between the vegetation processes and character of the microsites available for colonization (Table 2) leads to almost limitless possibilities for interactions. At La Pérouse Bay, the disturbance generated by geese and accompanying abiotic stress can act as constraints at many stages of the regeneration process following loss of vegetation. Sustained grazing may have a detrimental effect on seed production (Bertness & Ellison 1987, Mulder & Harmsen 1995) as flowering and fruiting are much higher in sites protected from goose grazing for most species (Bazely & Jefferies 1986). This may, in turn, have a negative effect on seed numbers and the species composition of the seed rain. For instance, *C. subspathacea* spreads chiefly by rhizomes as it is rarely seen in flower outside of exclosures. The loss of vegetation and litter can alter the seed-trapping capabilities of a site in this often

windy, seasonally flooded environment. Soil erosion may lead to loss of seeds from the soil as most seeds are stored close to the surface. Finally, hypersaline soils can be detrimental to both the germination of seeds (Ungar 1978, Woodell 1985, Keiffer & Ungar 1997) and establishment of seedlings (Shumway & Bertness 1992).

Table 2. Processes involved in the successful invasion of a gap by a given plant species and characters of the gaps that may be important. Modified from Grubb (1977).

Processes	Characters
Production of viable seed	Time of formation
Flowering	Size and shape
Pollination	Orientation
Setting of seed	Nature of soil surface
Dispersal of seed	Litter present
Through space	Other plants present
Through time	Animals present
Germination	Fungi, bacteria and viruses present
Establishment	
Onward growth	

Further complications arise when one considers that both biotic and abiotic factors which may make a habitat suitable for seed storage in the seed bank may provide a less than ideal setting for seedling establishment (Schupp 1995), resulting in conflicting selection pressures for seeds and seedlings. A classic example concerns seed size. Small seed size allows for greater dispersability and thus, greater probability of escape from predators but small seeds also contain less reserves leading to, at least in theory, less competitive seedlings at the germination-establishment stages. In an alpine habitat in Montana, the soil particle sizes that produced highest entrapment and retention also led to little or no emergence for most species (Chambers 1995a). At La Pérouse Bay, highest entrapment and retention of seeds occur in undisturbed habitats, but establishment is subject to potential competition from adult plants.

1.5 Seed bank dynamics and revegetation at La Pérouse Bay

The salt-marsh vegetation at La Pérouse Bay, before the onslaught of current soil degradation processes, consisted largely of perennial vegetation. The two dominant graminoids, *P. phryganodes* and *C. subspathacea*, propagate mainly through stolons and rhizomes respectively. Both are also capable of generating adult plants from the dispersal of plant fragments (Chou *et al.* 1992). In addition, *P. phyrganodes* is a sterile triploid and has never been known to set seed (Bowden 1961) and, as mentioned above, *C. subspathacea* rarely sets seed outside of exclosures due to the heavy grazing pressure exerted by geese. Dicotyledonous plants found commonly in undamaged sites, such as the stoloniferous species, *Potentilla egedii* and *Stellaria humifusa*, also spread through clonal growth. The general stress of low temperatures, short growing season and high soil salinity appear to select for a regeneration strategy based on clonal propagation. In contrast to the intertidal and supratidal vegetation, the vegetation of the undamaged beach ridge is much more ruderal in composition (greater frequencies of *Matricaria ambigua, Atriplex patula* and *Stellaria longipes*) with the exception of the dominant species, *Leymus mollis*. The "weediness" of the plants may be linked to greater abiotic disturbance (wave-action, wind shear) and an unstable, sandy substrate.

In a degraded landscape, revegetation by clonal growth is expected to be very slow and difficult due to the very short range of dispersal mechanisms of clonal spread and the short survival period of plant fragments when no suitable microsites are available. However, a vegetative "template" of graminoids may be necessary in order for subsequent plant development, as many of the dicotyledonous species found in the original vegetation do not establish directly on bare mineral soils and the primary

colonizers in these salt marshes are the two dominant forage species. A study of the revegetation potential of the two dominant graminoids, *P. phryganodes* and *C. subspathacea*, at La Pérouse Bay indicated that *P. phryganodes* was able to establish unassisted on bare sediments in the intertidal salt marsh at sites where geese had been excluded since 1992 (Handa 1998). No revegetation, assisted or otherwise, was possible in the inland salt marshes. Once established, *P. phryganodes* can act as a "nurse" plant and trap seed and vegetative fragments from the strand line, seed rain and snow melt. The "template" of *P. phryganodes* lowers the soil salinity considerably and provides a more hospitable environmental for establishment.

The primary objectives in this study were to examine the relationship between the vegetation and soil seed bank, and the mechanisms underlying this relationship in the context of a northern salt marsh. The secondary objective, to determine revegetation potential, can be fulfilled as a corollary to the observation of how regeneration processes of plant communities subject to high levels of stress respond when additionally exposed to high levels of disturbance.

When considering the role of seed banks in revegetation, "success" is linked to (1) the presence of preferred or required species in the seed bank, (2) the absence of unwanted "weedy" species in the seed bank and (3) the creation and maintenance of habitat conditions suitable for preferred species (van der Valk & Pederson 1989). In this study, the magnitude and composition of seed banks at La Pérouse Bay were determined in relation to the effects of loss of vegetation and soil degradation on the size and composition of the soil seed bank and its potential contribution to revegetation (Chapter Three). The seed bank-vegetation dynamics and the environmental constraints posed by

degradation at each stage are examined in Chapter Four. Seed identification, which is necessary in fulfilling these objectives, can be an esoteric occupation. A multiple-entry identification key based on morphological and ecological characters was developed using the DELTA system in order to facilitate identification (Chapter Two). The morphological information collected on seeds of different taxa was also used to discuss possible links between the morphology and the ecology of seeds.

Chapter Two: Seed flora of La Pérouse Bay, Manitoba, Canada; a DELTA database of morphological and ecological characters

2.1 Introduction

The eruption of soil seed bank publications (c.f. Vyvey 1989a, Vyvey 1989b, Thompson *et al.* 1997) in the last two decades indicates the growing interest in the role of diaspore dynamics in vegetation patterns and processes. Possible sources of plant propagules, which enable revegetation to occur where habitat destruction has taken place, are of special interest (Bakker *et al.* 1996a). With an increasing rate of anthropogenic habitat conversion on a global scale (Dobson *et al.* 1997), there is a need for tools with which to identify seeds and small fruits that might be suitable in revegetation schemes. However, regional seed floras are relatively scarce (Jensen 1998) and published seed keys may encompass only a narrow taxonomic group or groups of economic interest such as crops, weeds or forage species. In addition, binary keys can be difficult to use with seeds that have been stored in the soil since characters for identification are often arranged hierarchically and some properties such as colour, surface features of seed coats and attached appendages can quickly change in the soil environment. A multiple entry key (polyclave) based on characters easily distinguished under a compound light microscope can greatly facilitate the identification of potentially large numbers of seed samples. For sake of ease, the term, "seed," will be used to describe both true seeds and small, indehiscent fruits.

In studies of soil seed bank ecology, seed morphology has relevance beyond its application in identification. Morphological characters such as seed size and shape have

been linked to various aspects of seed ecology such as predation risk, dispersability, landing, seedling establishment, burial and persistence (Harper *et al.* 1970, Peart 1984, Thompson 1987, Westoby *et al.* 1990, Thompson *et al.* 1993, Westoby *et al.* 1996, Bekker *et al.* 1998b, Hodkinson *et al.* 1998). The possible association of morphological traits with persistence is of particular interest in disturbed soils because persistent seed banks are important in determining the potential for revegetation at these sites. Hence, a database of morphological and ecological characters could serve as a valuable starting tool in studying these links.

A study of the seed bank ecology of La Pérouse Bay, Manitoba was undertaken in May 1997 in order to explore the relationship between seed persistence and disturbance. Grubbing and grazing by increasing numbers of lesser snow geese *(Anser caerulescens caerulescens)* in the Hudson Bay lowlands have resulted in the conversion of coastal salt marsh into hypersaline mud flats largely devoid of vegetation (Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996, Jano *et al.* 1998). The need to identify seeds found in the soil profile and surface seed traps in relation to possible revegetation schemes led to the development of a DELTA (DEscriptive Language for TAxonomy) database.

The DELTA format is a versatile and effective tool for data storage and management of descriptive taxonomic data (Dallwitz 1980) while the DELTA system is an integrated set of programs based on the DELTA format. The DELTA format is currently the standard for data exchange by the Taxonomic Databases Working Group and has been used to describe organisms or biological materials as diverse as viruses (Boswell *et al.* 1986), insects, corals, crustaceans, fish, fungi (Thrane 1991), plant pollen (Vezey *et al.* 1991), plants (Aiken *et al.* 1996, Aiken *et al.* 1997) and wood (de Pernia & Miller 1991).

Using the DELTA programs, data (text, measurements, character-states) in the DELTA format can be converted not only into binary keys, distance matrices and natural language descriptions but also into multiple entry keys, permitting the user to carry out an identification using characters in any order. Polyclave programs that use DELTA-formatted data include both workstation based ones like INTKEY (Dallwitz *et al.* 1995) and PANKEY (http://www.rbge.org.uk/ research/pankey. html) and WWW-based ones such as PollyClave (http://prod.library. utoronto.ca/polyclave.html) and Navikey (http://www.herbaria.harvard.edu/computerlab/ web_keys/navikey/).

Here we document the seed flora of La Pérouse Bay in the form of 1) a checklist and 2) an illustrated DELTA database. The data are illustrated here with respect to selected characters and a multivariate summary. The entire DELTA database can be accessed on the WWW.

2.2 Materials and Methods

2.2.1 Data and specimen collection

Soil samples for the ecological studies of the seed bank were collected largely in the salt marshes, which are the primary feeding grounds of lesser snow geese. Samples were gathered from two long-term exclosures (exclosed from goose grazing since 1982) and ten damaged vegetation plots on the intertidal flats on the western coast of La Pérouse Bay, from five undamaged and five damaged paired vegetation plots on the eastern intertidal section of the Bay, from twenty undamaged and twenty damaged vegetation plots in the supratidal marsh and lastly from two long-term exclosures (exclosed from goose grazing since 1984) and two damaged vegetation plots paired with the exclosures in an inland salt

marsh 3 km from the coast. Sampling for the soil seed bank took place in the supratidal plots after spring melt in June 1997 and in other areas at the same time of year in 1998. At each plot, ten soil cores (diameter of 6.7 cm and a depth of 6cm) were taken randomly along a one-metre transect. The soil cores were then separated into two layers and pooled within layers resulting in approximately 1 litre of soil for each pooled layer sample.

The size and characteristics of the soil seed bank were measured using a modified seedling emergence technique (ter Heerdt *et al.* 1996) but the residual soil was sorted by hand under a microscope to identify viable seeds that did not germinate. Surface seed traps (30 cm by 30 cm squares of artificial lawn material) were used to sample the seed rain during the growing seasons of 1997 and 1998 and spring melt of 1998 and 1999 in the same plots used to sample for the seed bank in the supratidal marsh. Effort was made to collect seed specimens for all species found in the different plant assemblages present in the vicinity of La Pérouse Bay due to the possibility of seed dispersal into salt-marsh areas. Greater details of the sampling design, and the seed bank and seed rain data are given in Chapter 3.

Seed specimens were haphazardly and opportunistically sampled from plants as close to time of dispersal as possible during the summer of 1997 (N=55 species) and 1998 (N=5 species) at La Pérouse Bay. As many flowers fail to set seed in the Arctic (Bliss 1971), random sampling was not possible. When possible, specimens were gathered from different individuals and different locations. They were air-dried in the field, transported back to the laboratory and separated from parent material. For many species, an adequate number of specimens could not be found in the field due to the following: 1) species were rare, occasional (See Table 3) or difficult to find because of the extremely small stature of

many species, 2) seed production was low or irregular and many flowers failed to set seed as is common in arctic systems (Bliss 1971) or 3) fruiting and seed dispersal occurred after we left the site (less likely). The database was augmented with seeds collected from herbarium samples at the Royal Ontario Museum Vascular Plant Herbarium (TRT) (N=39 species). A slide-mounted collection of the seed specimens, along with plant voucher specimens, was deposited at TRT.

2.2.2 Database and key development

A database in the DELTA format consists minimally of three files: a specification file (SPECS) describing character traits (e.g. number of characters, character types), a character file (CHARS) and a taxon description file (ITEMS). Additional text files (e.g. CIMAGES) can be used to specify character illustrations or other information. Development of these files is greatly facilitated by the DELTA.EXE editor (Zurcher 1999) and the program for image annotation, INTIMATE.EXE.

The DELTA program CONFOR converts the text files referred to above into binary files. The directive TOINT was used to produce two binary files (ICHARS, IITEMS) for use in interactive identification. Natural language descriptions were generated from the CHARS and ITEMS files using the directive, TONAT. The distance matrix referred to below was generated using the directives file, TODIS, and the program, DIST.

2.2.3 Taxa

A preliminary species list of the flowering plants of La Pérouse Bay (Table 3) was

compiled by consulting Scott (1996), Johnson (1987) and Porsild & Cody (1980). Out of the 153 species on the list, data were collected from 102 species (Table 3) with better representation of dicotyledonous species compared with monocotyledonous species. Species absent from the specimen collection whose character states could be scored by consulting the literature were also included in the database (*Rubus chamaemorus*, *Mertensia maritima* and *Juncus balticus*). When possible, each collected species was defined as a separate taxon in the database since identification to the species level is important in seed ecology studies. The ecology of closely related species may be very different, as in the case of the halophyte, *Potentilla egedii*, and its fresh water relative, *P. palustris*. *P. egedii* is found in undamaged salt marshes, whereas *P. palustris* invades damaged sedge meadows and is an indicator of disturbance.

Table 3. Preliminary flowering plant species checklist for La Pérouse Bay. Frequency of species was assessed subjectively and includes five classes (dominant, abundant, frequent, occasional, rare) with qualifying prefix "locally" as described in Kershaw & Looney (1985). Identification (I.D.) numbers were assigned for species contained in the database. *Arctostaphylos* spp., *Hippuris* spp., *Salix* spp. & *Stellaria* spp. were ultimately collapsed into genera in the database. Nomenclature follows Cody (1996). If the species was not in Cody (1996), then nomenclature follows Porsild & Cody (1980).

Species	I.D. Number (Fig. 8)	Frequency
Monocotyledoneae		
1. *Alopecurus alpinus* J.E. Smith		
2. *Amerorchis rotundifolia* (Banks) Hultén		rare
3. *Arctagrostis latifolia* (R. Br) Griseb. s.l.		rare
4. *Arctophila fulva* (Trin.) Rupr.		
5. *Calamagrostis canadensis* (Michx.) Beauv.		occasional
6. *deschampsioides* Trin.		locally abundant
7. *stricta* (Timm) Koeler		frequent

Table 3 (cont.)

Species	I.D. Number (Fig. 8)	Frequency
8. *Carex aquatilis* Wahlenb.	1	dominant
9. *canescens* L.		
10. *capillaris* Löve *et al.*	3	
11. *consimilis* Holm	2	
12. *glareosa* Wahlenb. var. *amphigena* Fern.		
13. *gynocrates* Wormskj.	4	
14. *microglochin* Wahlenb.		
15. *marina* Dewey		
16. *rariflora* (Wahlenb.) Sm.		
17. *saxatilis* L.		
18. *subspathacea* Wormskj.	5	locally dominant
19. *vaginata* Tausch		
20. *Corallorhiza trifida* Chat.	6	occasional
21. *Dupontia fisheri* R. Br. ssp. *psilosantha* (Rupr.) Hult.		frequent
22. *Eleocharis acicularis* (L.) R. & S.		
23. *Eriophorum angustifolium* Honckn.	8	locally frequent
24. *callitrix* Cham.		rare
25. *Festuca rubra* L. s.l.	9	locally abundant
26. *Hierochloë hirta* (Schrank) Borbas ssp. *arctica* G. Weim.	10	locally frequent
27. *Hordeum jubatum* L.	11	occasional
28. *Juncus arcticus* Willd.	13	occasional
29. *balticus* Willd. var. *littoralis* Engelm.	14	occasional
30. *bufonius* L. s.l.	15	frequent
31. *castaneus* Smith	16	occasional
32. *triglumis* L. ssp. *albescens* (Lange) Hultén	12	occasional
33. *Kobresia simpliciuscula* (Wahlenb.) Mack.		
34. *Leymus mollis* (Trin.) Pilger ssp. *villosissimus* (Scribn.) A. Löve	7	locally abundant
35. *Luzula confusa* Lindb.		
36. *groenlandica* Böcher		
37. *Maianthemum trifolium* (L.) Sloboda	22	rare
38. *Platanthera obtusata* (Pursh) Lindl.		occasional
39. *hyperborea* (L.) R. Br.		occasional
40. *Poa alpina* L.		
41. *arctica* R. Br.		
42. *Potamogeton alpinus* Balbis ssp. *tenuifolium* (Raf.) Hultén	18	rare

Table 3 (cont.)

Species	I.D. Number (Fig. 8)	Frequency
43. *Potamogeton filiformis* Pers. var. *borealis* (Raf.) St. John	19	locally abundant
44. *Puccinellia nuttalliana* (Schult.) Hitchc.	20	locally abundant
45. *phryganodes* (Trin.) Scribn. & Merr.		locally dominant
46. *Rhynchspora alba* (L.) Vahl		
47. *Scirpus caespitosus* L. ssp. *austriacus* (Pallas) Asch. & Graeb.	21	frequent
48. *rufus* (Huds.) Schrad. var *neogaeus* Fern.		
49. *Sparganium hyperboreum* Laest.	23	occasional
50. *Spiranthes romanzoffiana* Cham & Schlecht.		occasional
51. *Tofieldia pusilla* (Michx.) Pers.	24	occasional
52. *Triglochin maritimum* L.	25	occasional
53. *palustre* L.	26	locally frequent
54. *Trisetum spicatum* (L.) Richt. var. *maidenii* Fern.		
Dicotyledoneae		
55. *Achillea nigrescens* (E. Mey) Rydb.		abundant
56. *Andromeda polifolia* L.	27	locally frequent
57. *Androsace septentrionalis* L.	28	rare
58. *Arabis alpina* L.		rare
59. *Arctostaphylos alpina* (L.) Spreng.	32	occasional
60. *rubra* (Rehd. & Wils.) Fern.	33	locally frequent
61. *uva-ursi* (L.) Spreng. s.l.	34	locally frequent
62. *Arnica angustifolia* Vahl in Hornem. ssp. *attenuata* (Greene) Douglad & Ruyle-Douglas		rare
63. *Astragalus alpinus* L.	35	occasional
64. *Atriplex glabriuscula* Edmonston		occasional
65. *patula* L.	36	locally abundant
66. *Bartsia alpina* L.	37	locally frequent
67. *Betula glandulosa* Michx.	38	locally abundant
68. *Cardamine pratensis* L. s.l.	102	occasional
69. *Castilleja raupii* Pennell s.l.	39	locally frequent
70. *Cerastium alpinum* L.	40	occasional
71. *Chrysanthemum arctium* L. ssp. *polare* Hultén	41	occasional

Table 3 (cont.)

Species	I.D. Number (Fig. 8)	Frequency
72. *Chrysosplenium tetrandum* (Lund) Fries	103	rare
73. *Cochlearia officinalis* L. ssp. *groenlandica* (L.) Porsild	104	rare
74. *Draba alpina* L.		rare
75. *Dryas integrifolia* M. Vahl ssp. *integrifolia*	42	locally frequent
76. *Empetrum nigrum* L. ssp. *hermaphroditum* (Lge.) Böcher	43	locally frequent
77. *Epilobium angustifolium* L. s.l.	44	locally abundant
78. *latifolium* L.	45	occasional
79. *palustre* L.	46	rare
80. *Erigeron elatus* (Hook.) Greene		occasional
81. *Euphrasia arctica* Lge.	47	frequent
82. *Gentianella propinqua* (Richards.) J. M. Gillett ssp. *propinqua*	48	occasional
83. *Hippuris tetraphylla* L. f.	49	locally abundant
84. *vulgaris* L.	50	locally abundant
85. *Honkenya peploides* Ehrh. var. *diffusa* (Hornem.) Mattf.	51	locally abundant
86. *Kalmia polifolia* Wang. s.l.	52	occasional
87. *Koenigia islandica* L.	105	rare
88. *Ledum decumbens* (Ait.) Lodd.	53	locally frequent
89. *groenlandicum* Oeder		rare
90. *Lesquerella arctica* (Wormskj.) S. Wats.		rare
91. *Lomatogonium rotatum* (L.) Fries ssp. *rotatum*	54	locally frequent
92. *Matricaria ambigua* (Ledeb.) Kryl.	55	abundant
93. *Menyanthes trifoliata* L.	56	occasional
94. *Mertensia maritima* (L.) S.F. Gray	57	rare
95. *Minuartia rubella* (Wahlenb.) Graebn. ex Asch. & Graebn.	58	locally frequent
96. *Moehringia lateriflora* (L.) Fenzl		rare
97. *Myrica gale* L.	59	locally abundant
98. *Myriophyllum sibiricum* Komarov	60	occasional
99. *Orthilia secunda* (L.) House s.l.		occasional
100. *Parnassia kotzebuei* Cham. & Schlecht.	61	rare
101. *palustris* L.	62	abundant
102. *Pedicularis flammea* L.	63	occasional
103. *groenlandica* Retz.		rare

Table 3 (cont.)

Species	I.D. Number (Fig. 8)	Frequency
104. *Pedicularis labradorica* Wirsing	64	occasional
105. *lapponica* L.	65	occasional
106. *sudetica* Willd. s. lat.	66	locally frequent
107. *Petasites sagittatus* (Banks ex Pursh) Gray	67	abundant
108. *Pinguicula vulgaris* L.	68	frequent
109. *Plantago maritima* L. s.l.	69	locally frequent
110. *Polygonum viviparum* L.	70	occasional
111. *Potentilla egedii* Wormskj.	71	locally frequent
112. *norvegica* L.		
113. *palustris* (L.) Scop	72	locally abundant
114. *pulchella* R. Br.	73	occasional
115. *Primula egaliksensis* Wormsk.	74	locally abundant
116. *incana* M. E. Jones	74	locally abundant
117. *Pyrola grandiflora* Radius	75	locally frequent
118. *Ranunculus aquatilis* L. var. *aquatilis*	76	occasional
119. *cymbalaria* Pursh.	77	frequent
120. *gmelini* DC. ssp. *purshi* (Richards.) Hultén	78	occasional
121. *lapponicus* L.		occasional
122. *pedatifidus* Sm.		rare
123. *Rhinanthus minor* L. ssp. *borealis* (Sterneck) A. Löve	79	locally frequent
124. *Rhododendron lapponicum* (L.) Wahlenb.		locally frequent
125. *Ribes oxyacanthoides* L.		rare
126. *Rubus arcticus* L. ssp. *acaulis* (Michx.) Focke	81	occasional
127. *chamaemorus* L.	80	occasional
128. *Rumex occidentalis* S. Wats.	82	frequent
129. *Sagina nodosa* (L.) Fenzl var. *nodosa*	83	rare
130. *Salicornia borealis* Wolff & Jefferies	106	locally abundant
131. *Salix arctophila* Cockerell	84	occasional
132. *brachycarpa* Nutt. ssp. *brachycarpa*	85	locally abundant
133. *candida* Flügge	86	locally abundant
134. *lanata* L. ssp. *richardsonii*	87	locally abundant
135. *myrtillifolia* Anderss.	88	locally abundant

Table 3 (cont.)

Species	I.D. Number (Fig. 8)	Frequency
136. *Salix planifolia* Pursh. ssp. *planifolia*	89	locally abundant
137. *reticulata* L.	90	frequent
138. *Saxifraga aizoides* L.		rare
139. *caespitosa* L. s.l.	91	occasional
140. *cernua* L.		rare
141. *hirculus* L.	92	locally frequent
142. *oppositifolia* L.	93	occasional
143. *tricuspidata* Rottb.	94	occasional
144. *Senecio congestus* (R. Br.) DC.	95	abundant
145. *pauperculus* Michx.	96	locally frequent
146. *Shepherdia canadensis* (L.) Nutt.	97	rare
147. *Silene apetalum* (L.) Fenzl.		rare
148. *Spergularia marina* (L.) Griseb.	98	locally frequent
149. *Stellaria humifusa* Rottb.	99	locally frequent
150. *longipes* Goldie s.l.	100	frequent
151. *Suaeda maritima* (L.) Dumort		rare
152. *Taraxacum ceratophorum* (Ledeb.) DC. s.l.	101	rare
153. *Vaccinium vitis-idaea* L. ssp. *minus* (Lodd.) Hultén		locally frequent

Note: *Primula egaliksensis* and *P. incana* have the same number as they hybridize regularly and these two species and their hybrids are difficult to distinguish when in fruit. states were recorded based on direct observations, measurements and from literature

2.2.4 Characters

The character list (Appendix 1) was compiled by consulting published seed keys (Fiske 1935, Martin & Barkley 1961, Okada 1964, Berggren 1969 and 1981, Hatusima & Yoshinaga 1970, Monod 1974, 1977 and 1979, Montgomery 1977, Bergstrom 1986, Anderberg 1994) and by examining specimens for suitable characters and selecting pertinent ecological information. Characters can be divided into two broad groups: morphological and ecological.

For morphological characters, the emphasis was placed upon characters that allow

quick and easy identification of many distantly related taxa. Morphological character states were recorded based on direct observations, measurements and from literature sources. When seeds of a species were available, ten seeds of each taxon were used to obtain the morphological data. Specimens were observed under a dissecting light microscope (Leica MS 5) in order to score "shape modifier" (characters 1 to 4 in Appendix 1) and "shape" characters (characters 7 and 8 in Appendix 1). As the aim of the database was to be able to identify seeds found both shortly after primary dispersal (seed rain) and buried in the soil (seed bank), the encoding of the presence or absence of "shape modifier" characters was flexible in the database. Many seed attachments (e.g. hairs, wings, bracts, styles) are unlikely to survive burial although they may be found on seeds trapped above ground. When such a discrepancy occurred, the character state was recorded as either present or absent.

Both planar and cross-sectional orientations were used in an effort to capture the three-dimensional shape of the seed when describing their shape. In order to score planar shape character, seeds were placed in a position where they lay as flat as possible and the hilum (indicating the point of placental attachment) was arbitrarily set as the base. For determining the cross-sectional shape, seeds were cut at the widest point perpendicular to the length of the seed. No particular orientation was set for the cross-sectional shapes. Terminology of the planar and cross-sectional shapes of seeds followed guidelines given by the Systematics Association Committee for Descriptive Terminology (1962).

For measurements of seed size, seed outlines were digitized using a video camera (SONY AVC-D5 with AC adapter CMA-D5) connected to a monitor (SONY PVM-1343Q) and the framegrabber (Imaging Technology Inc. PCVISIONplus) installed in a

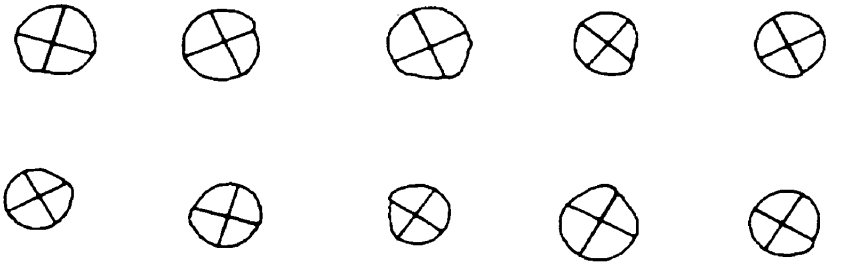
personal computer (Dell 310). This equipment, together with the program, MorphoSys (Meacham & Duncan 1993), allows the user to interactively obtain and measure the outlines of objects (Fig. 5). A compound light microscope (Polyvar) together with a camera and attached macro lens were used to magnify small and large seeds respectively. A range of values, usually the maximum and minimum, rather than the average, was used to represent the length and width of the taxa. Outliers (e.g. Fig. 6 *Cerastium alpinum, Euphrasia arctica, Ranunculus cymbalaria, Potentilla pulchella, Empetrum nigrum, Castilleja raupi, Senecio congestus, Honckenya peploides* and *Triglochin maritimum*; Fig. 7 *Epilobium palustre, Matricaria ambigua, Pedicularis labradorica, Pedicularis lapponica, Ranunculus gmelini, Carex subspathacea, Carex aquatilis* and *Menyanthes trifoliata*) were identified in the boxplots as values that fall at least 1.5 times the interquartile range above the third quartile or below the first quartile (Moore & McCabe 1993) and added as extreme values to the database.

"Seed surface" characters (characters 9 to 13 in Appendix 1) were scored by examining seeds under the compound light microscope. As some of the finer features were difficult to ascertain using light microscopy, the characters and states were described by consulting Stearn's *Botanical Latin* (1966) on the definition of taxonomic terms commonly used to describe surface features (e.g. areolate) and the illustrations of surface formations given in Murley (1951).

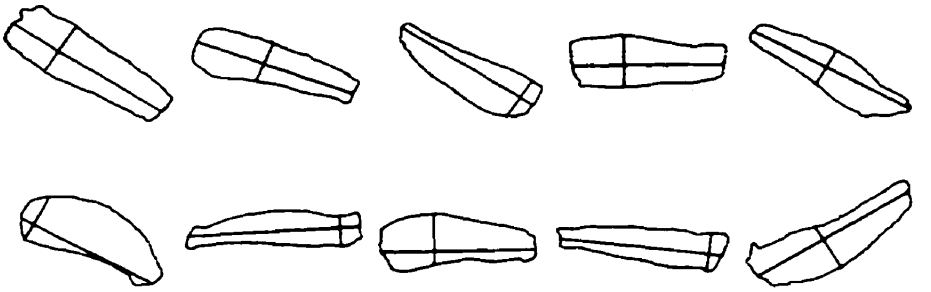
The ecological data consisted of two main groups: biogeography and soil seed bank ecology. The biogeographic data, including eco-region affiliation, were taken from Porsild & Cody (1980) and were included to help tailor the database to the needs of the user. While the broad geographic range is given in character 14, the dependent

Figure 5. Seed outlines showing examples of length and width measurements by MorphoSys. The hilum and the apex were determined visually and used as markers to measure length. The width was defined as the greatest distance perpendicular to the length. Although the degree of success with which MorphoSys captured these seed dimensions is variable, the method is far more accurate than those likely to be employed by users of this database.

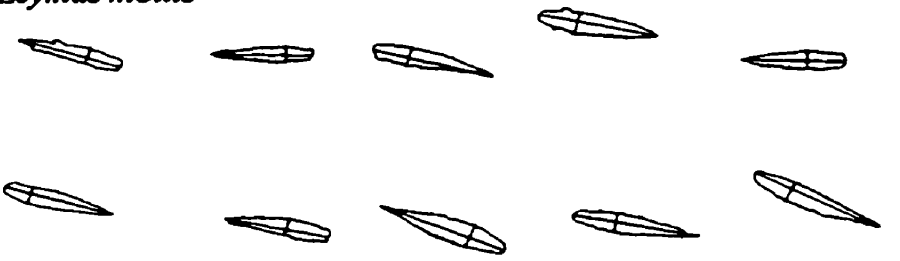
Atriplex patula



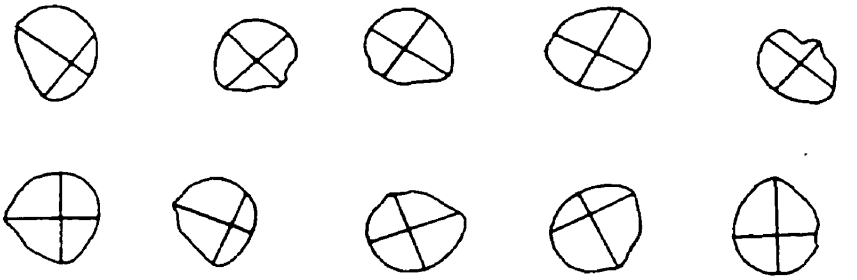
Chrysanthemum arcticum



Leymus mollis



Potentilla palustris



Ranunculus cymbalaria

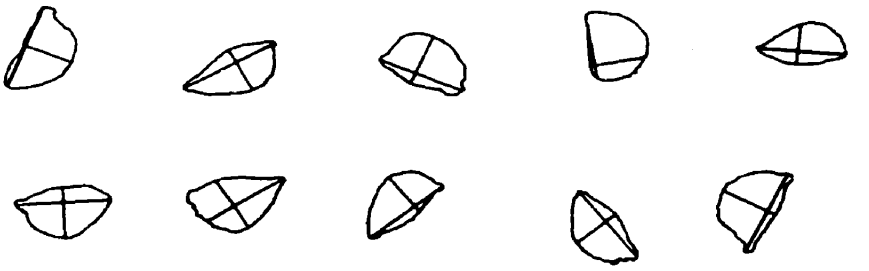


Figure 6. Length of seeds summarized in boxplots. The "whiskers" represent the range, the boxes represent the first and third quartiles and the horizontal lines within boxes represent the median. Outliers are identified with asterisks (*). Taxa are labeled using the first three letters of the genus and first four letters of the species name (for species name, consult Table 3 on pp. 33 to 38). Note changing scale of the y-axis.

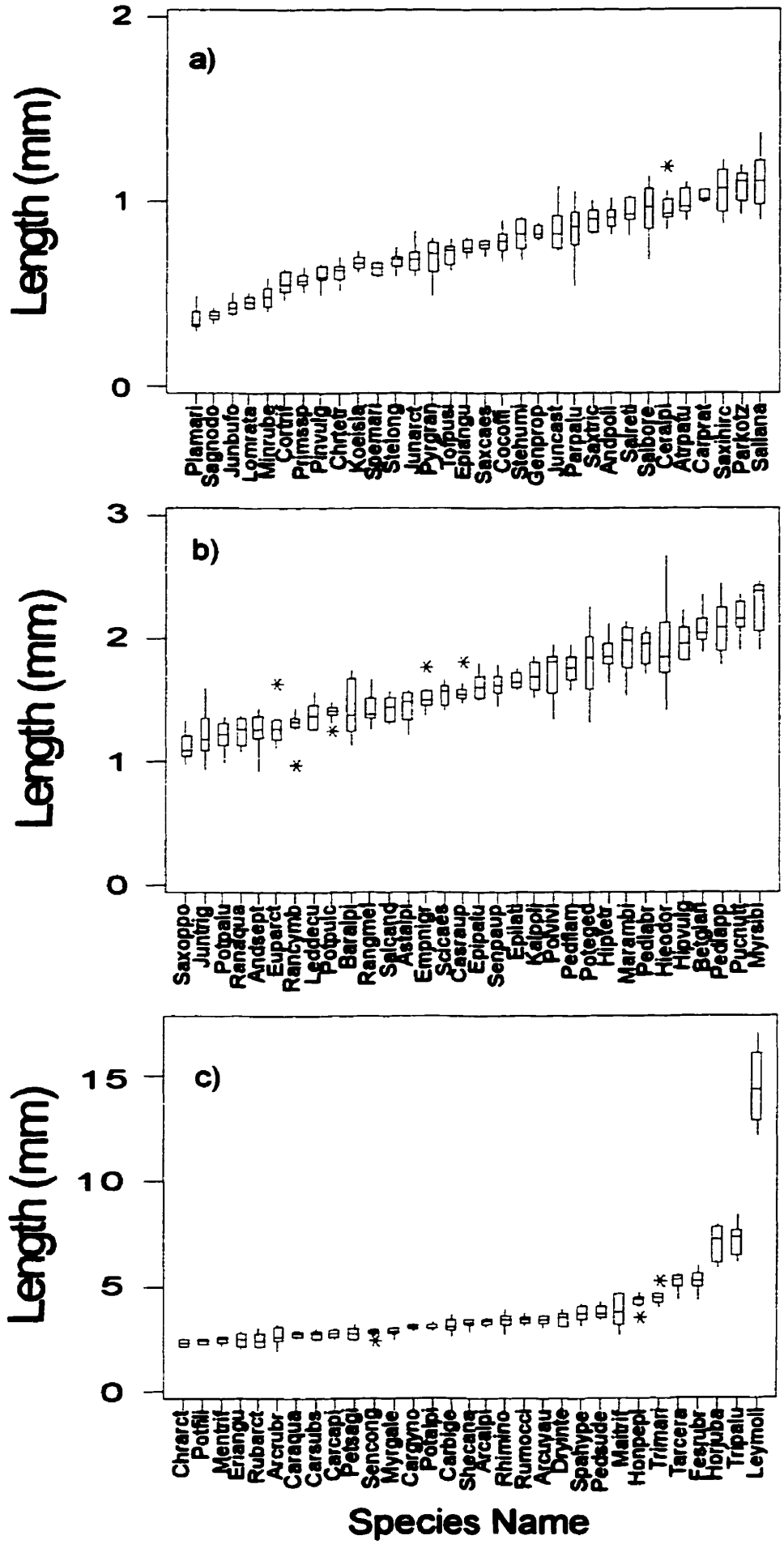
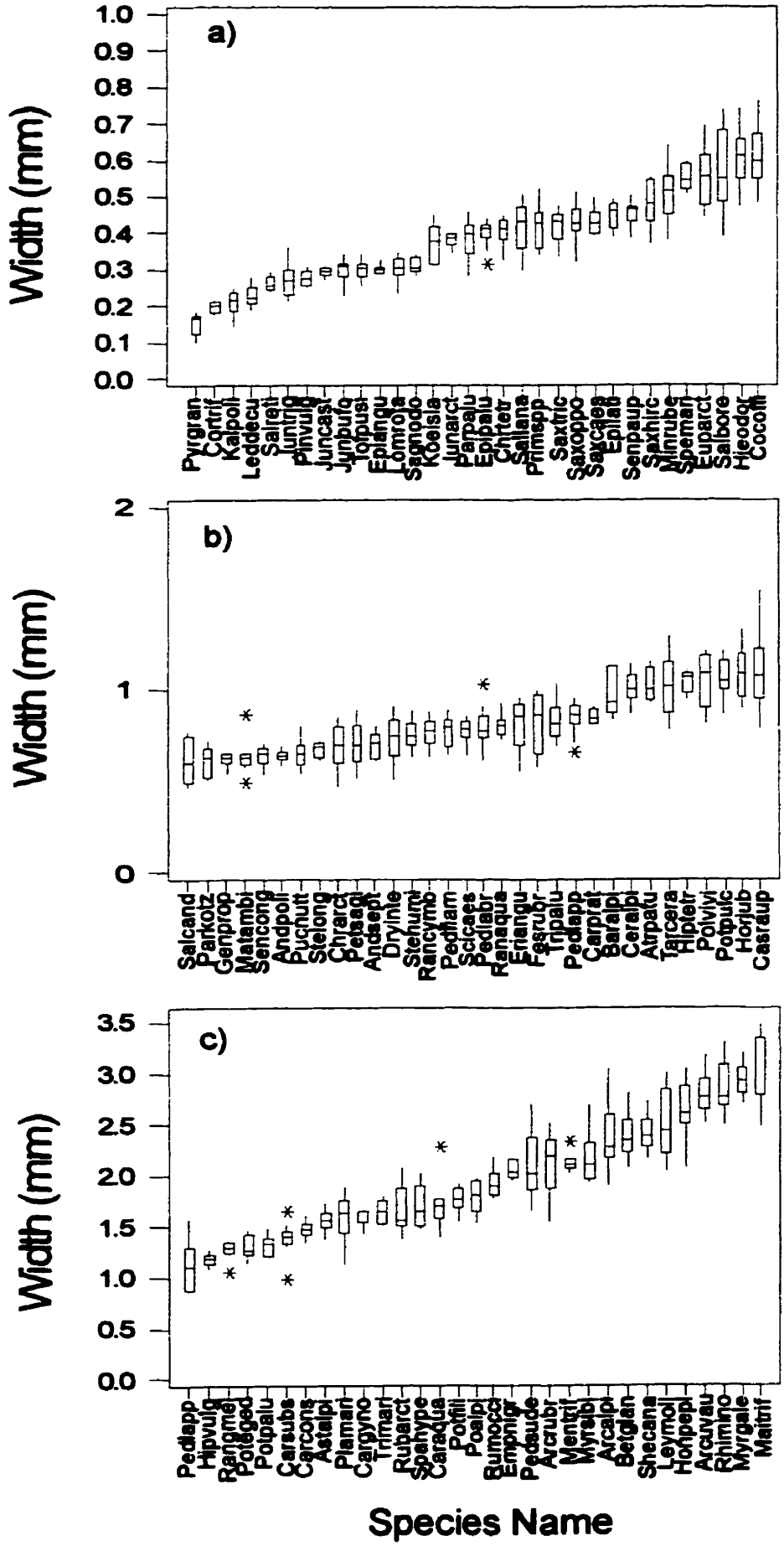

a)
Length (mm)
0
1
2
Plamari
Sagnodo
Junbufo
Lomrata
Minrubr
Cortri
Primsp
Pinvulg
Chrtet
Koelsia
Spemari
Sielong
Junarct
Pyrgran
Totpusi
Epilangu
Saxcaes
Cocom
Stehumi
Genprop
Juncast
Parpalu
Saxtric
Andpoli
Salred
Salbore
Ceralpi
Atrpatu
Carprat
Saxhirc
Parkotz
Sallana
b)
Length (mm)
0
1
2
3
Saxoppo
Juntrig
Potpalu
Ranaqua
Andsept
Eupatct
Ranrymb
Leddecu
Potpulc
Baralpi
Rangmel
Salgand
Astalpi
Empnigr
Scicaes
Casraup
Epipalu
Senpaup
Epilati
Kalpoll
Polvivi
Pedflam
Potpeg
Hiplet
Marambi
Pedlabr
Hieodor
Hipvulg
Betglan
Pedlapp
Pucrutt
Myrsbi
c)
Length (mm)
0
5
10
15
Chrarct
Potfili
Mentrif
Erlangu
Rubarct
Arcrubr
Caraqua
Carsubs
Carcapi
Petsagi
Sencong
Myrgale
Cargymo
Potalpi
Carbige
Shecana
Arcalpi
Rhimino
Rumocci
Acuyau
Drymle
Spahype
Pedsude
Maltrif
Honpepl
Trimari
Tarcera
Fesrubr
Horjuba
Tripalu
Leymoll
Species Name

Figure 7. Width of seeds summarized in boxplots. The "whiskers" represent the range, the boxes represent the first and third quartiles and the horizontal lines within boxes represent the median. Outliers are identified with asterisks (*). Taxa are labeled using the first three letters of the genus and first four letters of the species name (for species name, consult Table 3). Note changing scale of the y-axis.


a)
b)
c)
Width (mm)
Species Name

characters 15, 16 and 17 further isolate the ranges in North America, Europe and Asia. Presence or absence in the soil seed bank, seed rain and vegetation during the 1997/1998 sampling seasons in the salt marshes of La Pérouse Bay was recorded using binary valued dummy variables. Ecological data were included in order to allow qualitative, and eventually quantitative, comparisons with the morphological data. Most species possessed a wide range in the values recorded for density in the seed bank and seed rain, and frequency in the vegetation due to the sampling design (we sampled along a gradient of loss of vegetation and soil degradation) and the patchy distribution that is common for seeds in the soil (Thompson 1986, Thompson *et al.* 1997). Consequently, a binary scale (i.e. presence or absence), rather than actual density values or density classes, was used to describe the ecological data in this database. As noted above, most species in the database were absent from the above ground and below ground vegetation due to the sampling frame of the ecological data.

2.2.5 Multivariate data analysis

Only morphological characters (characters one to thirteen) were used in the multivariate analysis of the data. The DELTA program CONFOR, together with the directive file TODIS, and the program DIST were used to generate a semi-matrix of resemblances between taxa. The resemblance function employed is a modified version of Gower's coefficient (1971) for mixed data in its distance form (Dallwitz *et al.* 1993, pp. 84-85, 127). This coefficient has the advantage that it incorporates both multistate and measurement (i.e. continuously distributed) characters into a distance that has desirable geometric properties when used in cluster analyses (Legendre & Legendre 1983).

Average linkage clustering was then carried out using the SYN-TAX package (v. 5.03, Podani 1993) after first rearranging the distance matrix output by DIST so that it could be read successfully by SYN-TAX. This rearrangement was done using functions provided by the data analysis package S-Plus (v. 4.5 Rel. 2, MathSoft 1997).

The INTKEY functions, "similarities" and "differences," were used to further analyze relationships within the groups identified by cluster analysis. Both functions generate numerical and natural language descriptions of respective similarities and differences between taxa within clusters.

2.2.6 Illustrations

Seed taxa were photographed as slides using a compound light microscope and attached 35mm camera. Plant images were either photographed as slides in their natural habitats at La Pérouse Bay or obtained from the herbarium image collection at the TRT. TRT images were taken under natural light conditions or in studio settings. All slides were scanned using the Nikon 35mm Film Scanner LS-1000 and stored digitally as Joint Photographic Experts Group (JPEG) files. Images were cropped using Adobe Photoshop (Version 3.0) for Mackintosh computers and Paint Shop Pro 5 (Version 5.03) for Windows was used for further manipulations of the digitized images such as reorientation, compilation, scaling and annotations. The program INITIMATE, also part of the DELTA system, was used to associate the images with taxa and characters for INTEKEY and to add labels which can be turned on or off as desired.

2.3 Results

2.3.1 Taxa

Character state information was collected for 102 species but the diagnostic features of INTKEY indicated that some species were indistinguishable from each other on the basis of these characters. In some cases, species were collapsed into a genus taxon (*Arctostaphylos* spp., *Hippuris* spp., *Salix* spp. and *Stellaria* spp.) and in others, morphologically similar but more distantly related species were kept as separate taxa (*Corallorhiza trifida* and *Pyrola grandiflora*, *Tofieldia pusilla* and *Epilobium angustifolium*). In cases where some but not all members of a genus (*Pedicularis labradorica* and *P. lapponica*) or family (Ericaceae: *Kalmia polifolia* and *Ledum decumbens*) were indistinguishable, species were also kept as separate taxa. The final tally of taxa distinguished in the database was 92. As DELTA character and item files are easily modified, the database can be expanded with minimal effort to include missing species as they are collected.

2.3.2 Characters

The seed database and the generated identification key were used successfully to identify the two taxa found in the residual soil sorted after seedling germination had ceased (*Hippuris* spp. and *Potentilla egedii*) and seventeen out of twenty-one taxa caught in the seed traps (*Atriplex patula*, *Betula glandulosa*, *Carex aquatilis*, *Carex gynocrates*, *Hippuris* spp., *Juncus bufonius*, *Lomatogonium rotatum*, *Matricaria ambigua*, *Myrica gale*, *Potamogeton filiformis*, *Potentilla egedii*, *Potentilla palustris*, *Ranunculus cymbalaria*, *Salicornia borealis*, *Salix* spp., *Saxifraga hirculis* and *Senecio congestus*).

Seed dimensions followed by seed shape proved to be generally the most useful characters in identifying seeds found in both the residual soil and seed rain. They were especially important for seeds found in the residual soil as shape modifiers and seed surface features rarely survived burial.

Rather than separating them into discrete size categories, the dimensions, length (Fig. 6) and width (Fig. 7), formed a gradient with the exception of one taxon, *Leymus mollis*. Consequently, although the seed dimension characters are good characters diagnostically, they need to be measured with great accuracy and entered as a range including a margin of error. Here, the dimensions were obtained digitally and may be far more accurate and precise than manual measurements. When multiple specimens of taxa are available, it would be prudent to use average values. In terms of gross seed shape, most of the species had width to length ratios between 1:1 and 1:3 (Fig. 8). A few species had very long and narrow shapes with a width to length ratio around 1:6.

2.3.3 Multivariate data analysis

Cluster analysis using morphological traits resulted in 11 preliminary groups (Fig. 9). Three groups delineated plant families: Cyperaceae (group 1), Poaceae (group 3) and Asteraceae (group 5). All the Cyperaceae in the database were contained in group one. In contrast, group 3 contained only the smaller sized Poaceae with *Hordeum jubatum* and *Leymus mollis* in groups 10 and 11 respectively. All the Asteraceae were clustered in group 5 with the exception of *Matricaria ambigua*. Two taxa formed separate phenetic

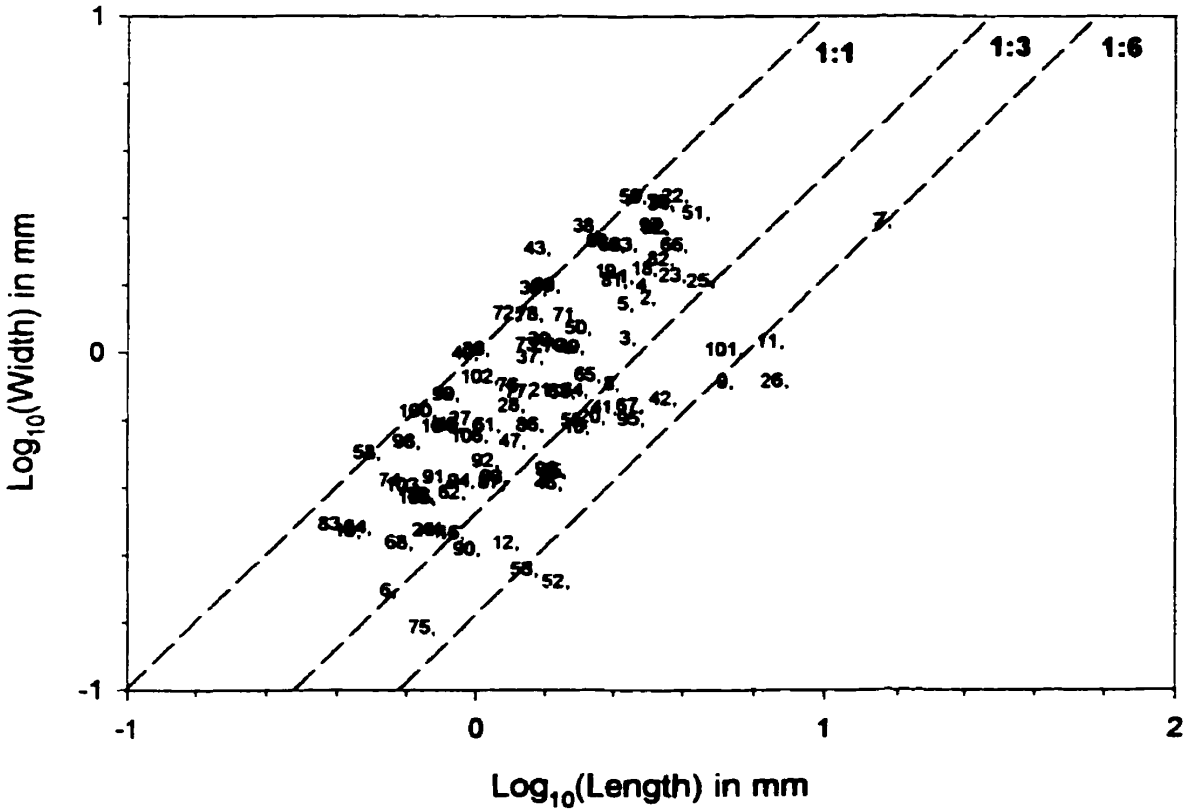
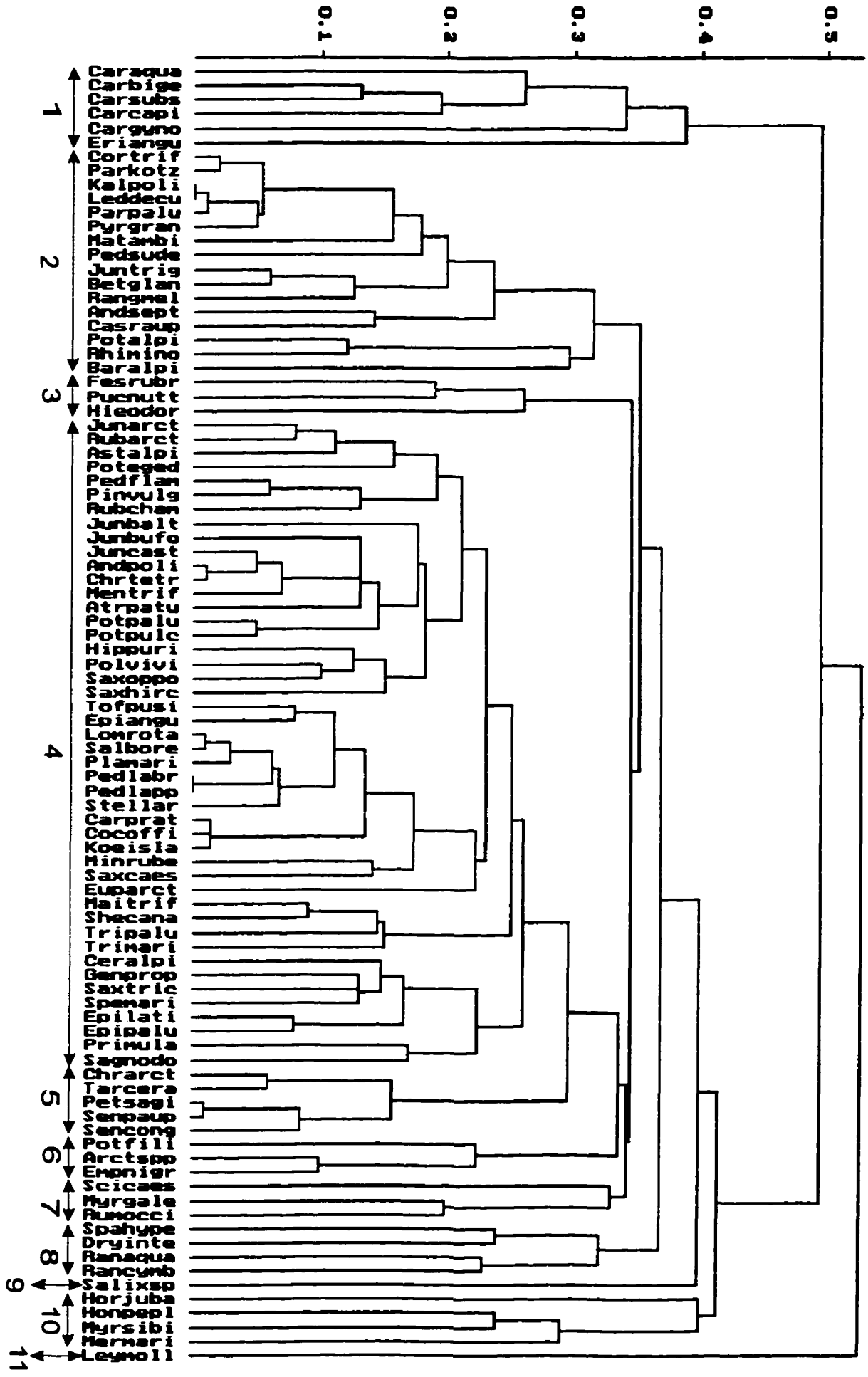


Figure 8. Log_{10} of seed width plotted against log_{10} of seed length showing width to length ratio. Data labels are identification numbers given in Table 3. Dashed lines represent width to length ratios of 1:1, 1:3 and 1:6.

Figure 9. Cluster analysis of seed morphological traits (characters one to thirteen in Appendix 1) using Gower's coefficient matrix. Eleven clusters are recognized and their descriptions are given in Table 4.


0.1
0.2
0.3
0.4
0.5
Caraqua
Carbige
Carsubs
Carcapi
Carguno
Eriangu
Cortrif
Parkotz
Kalpoli
Leddecu
Parpalu
Pyrgran
Matambi
Pedsude
Juntrig
Betglan
Rangmel
Andsept
Casraup
Potalpi
Rhinino
Baralpi
Fesrubr
Pucnutt
Hieodor
Junarct
Rubarct
Astalpi
Poteged
Pedflan
Pinvulg
Rubchan
Junbalt
Junbufo
Juncast
Andpoli
Chrtetr
Mentrif
Atrpatu
Potpalu
Potpulc
Hippuri
Polvivi
Saxoppo
Saxhirc
Tofpusi
Epiangu
Lomrota
Salbore
Planari
Pedlabr
Pedlapp
Stellar
Carprat
Cocoffi
Koeisla
Minrube
Saxcaes
Euparct
Maitrif
Shecana
Tripalu
Trinari
Ceralpi
Genprop
Saxtric
Spemari
Epilati
Epipalu
Primula
Sagnodo
Chrarct
Tarcera
Petsagi
Senpaup
Senconq
Potfili
Arctspp
Empnigr
Scicaes
Myrgale
Rumocci
Spahype
Dryinte
Ranaqua
Rancymb
Salixsp
Horjuba
Hompepl
Myrsibi
Marmari
Leymoll
1
2
3
4
5
6
7
8
9
10
11

groups: *Salix* spp. (group 9) and *Leymus mollis* (group 11). *Leymus mollis* was parted from the other species at the first separation due to its substantially larger size (Fig. 6c) but the reason *Salix* spp. were separated from groups 2 to 8 is unclear.

Description of the similarities and differences between taxa within the 11 groups are given in Table 4. The presence of seed shape modifier characters was important in defining groups 1 to 3 and 8. Group 5 had low width to length ratios. Groups 5 to 11 had taxa with generally larger sizes. With the exceptions of *Salix* spp. and *Ranunculus* spp., these taxa had lengths longer than the median length for the database. The largest cluster, group 4, contained species with generally elliptic, ovate or obovate shapes that lacked shape modifiers.

Table 4. Description of groups resulting from cluster analysis of morphological characters. Within-group "similarities" and "differences" were generated by INTKEY.

Group	Similarities	Differences
1	1. Cyperaceae 2. All have bracts except *Eriophorum angustifolium* 3. All have styles 4. Medium large size (length=2.01 mm to 3.73 mm) 5. Planar seed shape elliptic, ovate or obovate	1. Variable cross-sectional seed shape
2	1. All have wings/margins except for *Matricaria ambigua*	1. Large variation in size 2. Variable planar and cross-sectional seed shape
3	1. Small Poaceae 2. All have bracts 3. Planar seed shape elliptic 4. Larger seeds (length=1.42 mm to 5.99 mm)	

Table 4 (cont.)

Group	Similarities	Differences
4	1. Few species with seed shape modifiers (only 4) 2. Cross-sectional seed shape mostly elliptic 3. Planar seed shape elliptic, ovate or obovate	1. Large variation in size
5	1. Most of Asteraceae 2. No seed shape modifiers except hairs 3. Long and narrow shape	
6	1. No seed shape modifiers 2. Planar seed shape elliptic 3. Cross-sectional seed shape triangular 4. Larger seed size (length=1.37 mm to 3.73 mm)	
7	1. No wings or styles 2. Larger seed size (1.41 mm to 3.83 mm)	1. Variable planar and cross-sectional seed shape
8	1. All have styles, no bracts 2. Planar and cross-sectional seed shape elliptic	1. Variable seed size
9	1. *Salix* spp. 2. Hairs absent but indication of attachment 3. All have styles	
10	1. No seed shape modifiers except for hairs 2. Large seed size (length=1.9 mm to 7.95 mm) 3. Planar seed shape elliptic, ovate or obovate	1. Cross-sectional seed shape variable
11	1. *Leymus mollis* 2. Largest seed size	

2.3.4 Illustrations

The database includes 12 composite pictures illustrating character states, 87 photographs of seeds and 40 illustrations of plant species, both close-up and in their natural habitat. Effort was made to illustrate each taxon with a picture of the seed and the plant. Illustrations of taxa will be added to the database as they become available.

2.3.5 Availability of database

The DELTA-formatted database for the seed flora of La Pérouse Bay can be obtained by contacting the first author (echang@botany.utoronto.ca). The database can be consulted in its entirety on the World Wide Web by means of PollyClave, a web-based tool for interactive identification (http://prod.library.utoronto.ca/polyclave.html). The DELTA programs used in constructing and analyzing the database (the DELTA editor, CONFOR, DIST, etc.), and in using it for local interactive identification (INTKEY) can be obtained at http://biodiversity.uno.edu/delta/.

2.4 Discussion

The generated identification key and the multivariate summary of seed morphological traits form a strong foundation on which to build studies of the ecology of seed banks. Further uses of the multivariate summary would be to evaluate the identified groups on basis of their ecological function. Simple correlations that have been recognized between the ecology of seeds and their morphology include the ability to form persistent seed banks where seeds are small and have isodiametric shapes (Bekker *et al.* 1998b), and the ability to disperse if seeds have wings or a pappus. In the seed ecology studies at La Pérouse Bay, *Juncus bufonius* (group 4) and *Ranunculus cymbalaria* (group 8), both species with small seeds, had substantial and persistent seed banks. Species with wings or hairs, *Betula glandulosa, Senecio congestus* and *Salix spp.*, were also found to form a significant portion of the seed rain. Hence, examples exist where there are links between a morphological trait and its ecological function. However, consider that half the taxa in the database (N=46) are contained in group 4. Group 4 is generally characterized by small

(length<2.5mm with the exception of 4 taxa), round seeds that lack any obvious dispersal or landing mechanism. If a generic seed can be said to exist, this would be the description. Of the eleven taxa in group 4 that are commonly found in salt marshes, four were found solely in the seed bank (*Stellaria* spp., *Triglochin palustris*, *Spergularia marina* and *Primula* spp.), five were found in both the seed bank and seed rain (*Potentilla egedii*, *Juncus bufonius*, *Atriplex patula*, *Hippuris* spp. and *Salicornia borealis*) and two taxa were found in neither in the seed bank or seed rain (*Triglochin maritimum* and *Plantago maritima*). Note that *T. maritimum* and *T. palustris* do not fit the general morphological syndrome of group 4, being the only members with long and narrow shapes.

The relationship between seed ecology and seed morphology is mitigated by a number of different factors. Seed morphology contains many "trade-offs" between seed dispersability, landing, packaging of resources, escape from predation and movement through the soil column (Harper *et al.* 1970). The seed ecology of a species is affected by seed physiology, life history and disturbance regime as well as seed morphology. Increasing habitat disturbance was linked to increasing seed persistence for the flora of north-west Europe (Thompson *et al.* 1998). However, increased seed persistence was but not always linked to shifts in seed size in the north-west European flora. Plowing has broken the link between probability of burial and seed morphology in agricultural habitats (Thompson *et al.* 1998). In Australia, seed size and shape failed to predict seed persistence due to the fire disturbance regime (Leishman & Westoby 1998). In ecosystems dominated by fire disturbance, survival is often linked to a hard seed coat that typically results in a higher seed mass. In contrast, the link between seed size and morphology was supported in the British flora (Thompson *et al.* 1993, Hodkinson *et al.*

1998) and nine sites in five European countries (Netherlands, Sweden, Germany, Estonia and England in Bekker *et al.* 1998b) where disturbance regimes usually involve physical agitation of soil. At La Pérouse Bay, clear trends were difficult to discern between morphological groups as presently defined by average linkage cluster analysis and their presence in the soil seed bank, seed rain and seeds dispersed by spring floods. It should be noted, however, that soil degradation and resultant soil erosion also weaken the link between the initial probability of burial and survival.

Most studies on links between seed morphology and ecology have concentrated on one or two morphological traits and a specific ecological function. The identification of groups of seeds based upon many morphological factors complicates the relationship considerably and some characters, such as seed surface traits, may seem to have little ecological function. However, when these characters (9-13) were excluded from the analysis, DELTA was unable to generate a semi-matrix of resemblances between taxa due to the large number of taxa that became indistinguishable. Some surface characters are integral properties of the seed coat and may influence such important functions as moisture relations, flotation and interaction with small predators and pathogens. For example, some small seeds can be "unwettable", partly due to the existence of small pits filled with trapped air in the testa, and thus float on the surface of water (van der Pijl 1982). Such a property aids in dispersal by water.

It is acknowledged that the seed flora of La Pérouse Bay may be a highly specialized topic as only three known studies of seed ecology in the general vicinity have been conducted (Archibold 1984, Staniforth *et al.* 1998, Chapter 3 and Chapter 4). However, many arctic species have circumpolar distributions and 58 taxa in the database

have a circumpolar distribution. In addition, the types of genera found in salt marshes tend to be highly conserved as few plants are able to tolerate the high salinity. By setting the parameters for characters 14 to 18 (geographical distribution and eco-region) in INTKEY and PollyClave, the taxa can be filtered to include only those taxa with particular ranges (e.g. North America) or habitats (e.g. arctic and alpine). In this way, the database may be applied to regions beyond La Pérouse Bay.

As a subset of the flora of the Hudson Bay lowlands, the taxa of La Pérouse Bay are indicative of northern and coastal affinities, as outlined in Riley (1990). Nineteen of the forty-nine taxa restricted to the coast of the Hudson Bay lowlands, seventeen of fifty-four taxa restricted to the maritime tundra zone and twenty-one of fifty-four taxa restricted to the northern Hudson Bay lowlands are found at La Pérouse Bay. The checklist also contains nine native taxa classified as rare for the Hudson Bay lowlands (known from three or less locations out of total of eleven locations): *Calamagrostis deschampsioides, Juncus biglumis, Corallorhiza trifida, Koenigia islandica, Spergularia marina, Cochlearia officinalis, Lesquerella arctica* and *Suaeda maritima*.

Chapter 3: Effect of habitat degradation on the vegetation and seed bank in coastal salt-marsh and beach-ridge habitats

3.1 Introduction

At La Pérouse Bay and elsewhere in the Hudson Bay lowlands, the effects of the current high levels of disturbance and stress on plants, resulting from the foraging activities of large numbers of lesser snow geese, have led to loss of vegetation and the presence of degraded salt-marsh habitats with low plant diversity, low net primary productivity and high rates of soil erosion (Jano *et al.* 1998). Declines in plant standing crop and exposure of the underlying soil substrate on beach ridges have also been documented. Very few species can persist for any length of time under both high disturbance and high stress regimes (Grime 1979), and the only species that can be expected to survive under these conditions are stress-tolerant ruderals. However, seeds can often persist in soil as a "memory" of the former vegetation for a period of time (Bakker *et al.* 1996a), as they are often more tolerant of stress than their adult counterparts and, once buried in the soil, can escape some agents of disturbance, disease and predation. The survival of seeds of former communities under degraded conditions is determined by the relationships between the original plant assemblages, propagule production and seed reserves in the soil. All will be affected by the disturbance and stress regimes and the soil seed bank will decline as a function of the time that has lapsed since the vegetation was destroyed.

The highest similarity in species composition between vegetation and the seed bank is predicted when recruitment is tightly coupled to disturbance and secondary

succession follows the initial floristic development (Pierce & Cowling 1991). Where the vegetation regenerates through different successional phases after disturbance, or is characterized by gap-phase regeneration, the similarity is predicted to be low. For coastal dune vegetation in South Africa, the highest similarity was recorded for the most frequently disturbed community, the grassland, and the least frequently disturbed community, the thicket, had the lowest similarity between the vegetation and the seed bank (Pierce & Cowling 1991). In an alpine herb field on the Beartooth Plateau, Montana, the seed bank and the vegetation were the most similar in an early seral gravel borrow where medium-lived species dominated the plant community both above ground and below ground. In a late seral field, the vegetation was composed of mostly long-lived species while the seed bank was dominated by short-lived species (Chambers 1993).

Studies of the relationship between the vegetation and soil seed bank in different habitats have yielded highly variable results. In arctic and alpine habitats, the relationship was closely coupled for vegetation and seed banks on Mont Jacques-Cartier in Quebec (Morin & Payette 1988) and loosely coupled in a Scandinavian sub-arctic plant community and two central European alpine communities (Diemer & Prock 1993), an old-growth Colorado sub-alpine forest (Whipple 1978), a high sub-alpine site in the Oregon Cascade Mountains (Ingersoll & Wilson 1993) and coastal sub-arctic beach ridge, sand bar and salt-marsh sites near Churchill (Staniforth *et al.* 1998). For wetlands, similarities between the vegetation and seed bank were found in tidal fresh-water marshes (Leck & Graveline 1979, Parker & Leck 1985, Leck & Simpson 1987), coastal salt marshes (Hopkins & Parker 1984) and inland marshes (van der Valk & Davis 1978,

Pederson 1981). Dissimilarities were found in an Appalachian sphagnum bog (McGraw 1987), salt pans (Ungar & Riehl 1980) and a tidal fresh water marsh along the Delaware River (Leck & Simpson 1995).

The methods used to determine the similarity between the composition of the vegetation above ground and the seeds buried in the soil have also been various and numerous. They include qualitative assessments using the presence and absence of species (Morin & Payette 1988), percentage similarity (Ingersoll & Wilson 1993, Ungar & Woodell 1996), comparisons of frequencies (Leck & Simpson 1987, Diemer & Prock 1993, Leck & Simpson 1995), similarity indices (Sörensen's similarity index, van der Valk & Davis 1976, Grandin & Rydin 1998), correlation coefficients (Spearman's correlation coefficient, Grandin & Rydin 1998, Staniforth *et al.* 1998; Kendall's rank correlation coefficient, Pierce & Cowling 1991; community coefficient, Pierce & Cowling 1991), the X^2 goodness of fit test (Rydgren & Hestmark 1997) and the Mantel test (Jutila 1998). More recently, multivariate statistics have been used to summarize and assess the relationship (Bray & Curtis ordination, Jutila 1998; (detrended) correspondence analysis, Pierce & Cowling 1991, Looney & Gibson 1995, Rydgren & Hestmark 1997, Grandin & Rydin 1998; unweighted pair group mean cluster analysis, Ungar & Woodell 1996) but some difficulties arise due to the different scales used in measuring the vegetation (frequency and cover estimates) and the seed bank (density per unit area). One can circumvent the problem by comparing separate ordinations of the vegetation and the seed bank (Pierce & Cowling 1991, Looney & Gibson 1995) or reducing the data to presence or absence of species (Rydgren & Hestmark 1997). Grandin & Rydin (1998) simply noted the difference of scale in their ordination of seed

banks, former vegetation and current vegetation and made the comparisons with the axes rather than absolute similarity values. Many studies use multiple methods to assess similarity as the criteria have not yet been standardized.

In this study, redundancy analysis (RDA) (van denWollenberg 1977), a method largely neglected by ecologists (Jongman *et al.* 1987), was used to explore the relationship between the above ground plant community and the seeds stored in the soil. A form of reduced rank regression, RDA can be viewed as a constrained version of principal component analysis (PCA) (ter Braak 1994, Skinner *et al.* 1998). Canonical correlation analysis (CANCOR) may seem to be a more logical choice as it would produce the correlations and regressions for the relationship between the vegetation and seed bank and vice-versa in one ordination (Skinner *et al.* 1998). However, CANCOR has very stringent requirements regarding the ratio of samples to species that few ecological data sets can fulfill (Jongman *et al.* 1987). Two reciprocal RDA ordinations can be viewed as equivalent to CANCOR. Using RDA, the relationship between the vegetation and the seed bank can be explored in relation to gradients of disturbance, stress on plants and other potentially important environmental variables.

If disturbance (goose grazing, grubbing and soil erosion) and stress (hypersalinity and aridity) can be reduced and stabilized, what is the revegetation potential from the "memory" stored in the soil in damaged coastal salt-marsh and beach-ridge habitats? A study of the seed and vegetation dynamics in both undamaged and degraded habitats was undertaken to assess this potential. The relationship between vegetation and the soil seed bank was examined along a gradient of loss of vegetation and degradation of soil. The questions posed in this study are as follows: 1) What is the effect of loss of vegetation on

the soil seed bank? 2) What factors influence the time lag between the loss of vegetation and the loss of the seed bank? 3) What are the regeneration strategies of species characteristic of the undamaged salt marsh and invasive species? 4) To what extent can the below ground seed bank be predicted from the above-ground vegetation and vice-versa?

3.2 Materials and methods

3.2.1 Collection of seed bank and vegetation data

The soil seed bank and vegetation were sampled in intertidal, supratidal and inland salt marshes and on the beach ridge. Sampling areas were chosen *a priori* based on the presence of indicator species for each type of community. Species were chosen as indicators based on their efficacy in gauging underlying environmental gradients. For example, *Salicornia borealis* is an indicator of highly saline soils. The indicator species used to identify undamaged and degraded salt-marsh plots were *Potentilla egedii* and *S. borealis* respectively. On the beach ridge, closed swards of *Leymus mollis* indicated undamaged plots and *Matricaria ambigua* indicated degraded plots. For the salt-marsh community, samples were collected from two long-term exclosures (exclosed from goose grazing since 1982) and ten degraded vegetation plots on the intertidal flats on the western coast of the Bay, from five undamaged and five degraded paired vegetation plots on the eastern intertidal section of the Bay, from twenty undamaged and twenty degraded vegetation plots in the supratidal marsh and lastly from two long-term exclosures (exclosed from goose grazing since 1984) and two degraded vegetation plots paired with the exclosures in an inland salt marsh 3 km from the coast. No large patches (>9 m^2)

remain in the intertidal marsh on the west coast of the Bay. In the supratidal marsh, the twenty undamaged and degraded vegetation plots were blocked into two sites of ten plots each. In addition, ten undamaged and ten degraded paired plots were sampled on the beach ridge. Each set of paired plots, as well as the ten degraded plots on the intertidal flats on the west coast of the Bay and the twenty undamaged and twenty degraded vegetation plots in the supratidal marsh, were separated from each other by at least 25 metres.

The soil seed bank was sampled from supratidal areas after spring melt in June 1997 and from other areas at the same time of year in 1998. At each plot, ten soil cores (diameter of 6.7 cm and a depth of 6 cm) were taken randomly along a one-metre transect. The soil cores were then separated into two layers and pooled within layers resulting in approximately 1 litre of soil for each pooled layer sample. The soil cores were separated into layers because the distribution of seeds in the soil profile can be used as an indicator of longevity of seeds of individual species (Thompson *et al.* 1997). Where an organic horizon was visible, cores were separated into an upper organic and a lower mineral layer. The organic horizon was usually 2 to 3 cm in depth. Where only a mineral horizon was visible, the cores were separated into an upper and lower portion of equal size (i.e. 3 cm). Samples were assessed for seed bank using a modified seedling emergence technique (ter Heerdt *et al.* 1996). The seeds were concentrated by forcing the soils through a series of sieves (2mm, 220μm) with the use of a Honda water pump. The remaining soil and the seed concentrate were then spread out in trays (27cm by 53cm) on top of sterile silica sand, covered with ventilated cloches, placed in a common garden at La Pérouse Bay Field Station and monitored for seedling emergence. Trays

were watered and shaded from bright sunlight, as required; watering was necessary usually twice per day. Seedlings were removed from the trays as soon as identification was possible. Where identification was difficult, seedlings were transplanted into small flower pots (10cm in diameter), filled with a peat-marl mixture and further growth was monitored. At the end of the study, only a few seedlings remained unidentified. After approximately six weeks, the soils in the trays were dried, crumbled and then watered for an additional six weeks. Following completion of seedling emergence after a total of 12 weeks, sub-samples of the soils (10% by mass) were sorted under a dissection scope in order to detect apparent viable seeds that failed to germinate.

Corresponding percentage cover values were taken of the above ground vegetation in late July and early August, 1998 from the same plots where soil seed bank samples were collected. Due to time limitation, vegetation abundance was estimated by using a randomly chosen subset of the same plots used to sample the seed bank in the supratidal marsh (N=15 plots for undamaged and N=10 plots for degraded areas) and beach ridge (N=6 plots each for undamaged and degraded areas). At each plot, a grid (1m by 2m separated into 10cm x 10cm cells) was used to estimate cover values of vegetation. A pin was lowered at a random point within each 10cm x 10cm square and all species touching the pin were recorded. A total of 200 pin drops were recorded for each sample.

3.2.2 Collection of environmental data

Soil samples were collected in August, 1998 and 1999 respectively in order to determine the distribution of soil particle sizes and salinity. Three plots were picked randomly from

each of the undamaged and degraded sites sampled in the intertidal and supratidal salt marsh and on the beach ridge. Where only two plots were available, such as exclosures in western intertidal marsh at La Pérouse Bay, both were sampled.

Proportions of sand, silt and clay in the mineral soils were determined using the hydrometer method to measure particle size distribution (Sheldrick & Wang 1993). For soils of the inland marsh, which are rich in organic matter, such a measure was inappropriate. Soil particle size distribution data for the eastern intertidal salt marsh at La Pérouse Bay were taken from Handa (1998).

The soils were very dry in late July and early August of both years. Due to the difficulty of extracting pore water, a known volume of water was added to a known mass of soil and sodium concentrations (grams per gram of dry soil) were used as an index of salinity (Srivastava & Jefferies 1995a). Sodium content of the extract was measured using a Perkin-Elmer atomic absorption spectrophotometer (model 3110) in flame-emission mode.

3.2.3 Data analyses

The distribution of seeds is the soil is rarely normal (Thompson 1986, Thompson *et al.* 1997) and this was the case at the plots sampled at La Pérouse Bay in spite of the large sampling effort. The Wilcoxon rank-sum test (test statistic is W_n) modified for a two-way layout and including interaction terms (Bradley 1968) was used to compare the total seed bank (all species pooled) in the intertidal-marsh and beach-ridge plots, with respect to the status of vegetation loss and vertical distribution in the soil column. A general linear model, using the Poisson distribution, was used to test for differences in the seed

bank of the supratidal salt marsh as the sampling design was complex. The inland marshes could not be statistically analyzed due to the extremely small sample size (N=2 exclosures and paired degraded plots).

The relationship between the soil seed bank and above-ground vegetation was examined using a multivariate statistical method, redundancy analysis (RDA) (van den Wollenberg 1977). For the vegetation ordination, both floristic seed bank data and environmental variables were regressed onto the vegetation data. The seed bank data were first transformed, $y = \log(x + 1)$, and then the first eight PCA axes of the seed bank data were extracted. These principal coordinates or "super-species" were used as the floristic predictor variables rather than the raw seed bank data, in order to increase the sample to predictor variable ratio. Three soil variables, percentage sand, percentage silt and an index of soil salinity, were used as environmental variables. Bipartial canonical ordination was used to extract the unique portions of the vegetation data explained by the soil seed bank and environmental data (ter Braak 1988).

The same procedure outlined above was followed to predict seed bank data from vegetation and soil data. Comparison of the RDA results to random expectation based on Monte Carlo simulation (1000 permutations) was used to test for significance using the F-statistic (ter Braak 1986). The statistical program used for these analyses was CANOCO (ter Braak 1987).

3.3 Results

3.3.1 Vegetation

The vegetation consisted of 33 species that were assigned to a plant species assemblage type with which they had the closest association (Jefferies *et al.* 1979, E. Chang personal observation). Classification of species according to assemblage type was determined subjectively based on long-term observations of the vegetation at La Pérouse Bay and elsewhere in the Hudson Bay lowlands over a 20-year period. The plant assemblages found in undamaged salt marshes include a graminoid sward, dominated by *Puccinellia phryganodes* and *Carex subspathacea*, and a willow-grassland consisting *of Salix brachycarpa, S. myrtillifolia* and two caespitose grasses, *Festuca rubra* and *Calamagrostis deschampsioides*. The associated dicotyledonous species include *Potentilla egedii, Plantago maritima, Ranunculus cymbalaria, Stellaria humifusa* and *Stellaria longipes* for lower-lying graminoid swards and *Parnassia palustris, Lomatogonium rotatum, Rhinanthus borealis, Primula egaliksensis* and *Primula incana* on willow islands. Where vegetation is lost, *Salicornia minor* invades hypersaline mudflats along with *Spergularia marina* and *Atriplex patula*. Within the delta of the Mast River and where subsidiary streams of Wawao Creek feed into La Pérouse Bay, unconsolidated sediments in brackish ponds and streams are colonized by *Hippuris tetraphylla*. The "weedy" assemblage consists of ruderal species that are not tolerant of high soil salinity and includes *Senecio congestus, Matricaria ambigua, Rumex occidentalis, Juncus bufonius* and *Achillea nigrescens*. The beach-ridge vegetation is dominated by *Leymus mollis*.

Loss of vegetation and degradation of habitat resulted in a substantially lower vegetation cover for all plots (Tables 5-9) and shifts in species assemblage from greater relative abundance of characteristic salt-marsh or beach-ridge species to more ruderal species (Fig. 10). In intertidal, supratidal and inland salt marshes, the vegetation changed from lush graminoid swards with relatively high dicotyledonous species diversity to plots with low plant biomass that were invaded by weedy species such as *Senecio congestus*.

Eventually, vegetation was either lost entirely or was characterized by monocultures of *S. borealis*. The undamaged eastern intertidal plots had a high cumulative vegetation cover (100.2%) but extremely low dicotyledonous species diversity compared to other undamaged plots. Beach-ridge vegetation changed in response to disturbance from assemblages structurally dominated by *Leymus mollis*, a tall grass, to short vegetative cover composed mostly of *Matricaria ambigua*.

3.3.2 Soil seed bank

In general, total soil seed bank densities were highest in plots in the western intertidal marsh of the Bay (1740-10 700 seeds m^{-2}) and the beach-ridge (334-7490 seeds m^{-2}), followed by plots in the supratidal (11.4-2390 seeds m^{-2}), inland (100-2114 seeds m^{-2}) and eastern (28.6-126 seeds m^{-2}) salt marshes. Loss of vegetation and soil degradation did not significantly affect the seed density in soils, within each marsh area, compared with corresponding values for undamaged plots in the western intertidal marsh (Wilcoxon rank-sum test, n=2, m=10, W_n=18, n.s.) (Fig. 11a, b), the inland salt marsh (Fig. 11g, h) and the beach ridge (Wilcoxon rank-sum test, n=10, m=10, W_n=91, n.s.) (Fig. 12).

Table 5. Percentage cover (±standard error) of species in vegetation of undamaged and degraded plots in an intertidal salt marsh on the western coast of La Pérouse Bay. The undamaged plots have been exclosed from goose grazing since 1982.

Species	Undamaged Sites (N=2)	Degraded Sites (N=10)	Species Total (frequency/200)
Salt Marsh Graminoid Sward			
Carex subspathacea	82.50	9.55±3.48	92.05
Potentilla egedii	82.00	0.20±0.20	82.20
Puccinellia phryganodes	26.75	7.05±4.29	33.80
Stellaria longipes	26.00	0.2±0.11	26.20
Puccinellia nuttaliana	10.50	0	10.50
Ranunculus cymbalaria	6.75	1.50±0.40	8.25
Stellaria humifusa	2.00	0	2.00
Salt Marsh Willow-Grassland			
Festuca rubra	53.75	0.05±0.05	53.80
Calamagrostis deschampsioides	4.75	2.10±0.62	6.85
Salix brachycarpa	0	1.00±1.00	1.00
Salix spp.	0.25	0	0.25
Parnassia palustris	0	0.05±0.05	0.05
Lomatagonium rotatum	0	0.05±0.05	0.05
Hypersaline Mudflats			
Salicornia borealis	0.25	0	0.25
Brackish Marsh			
Triglochin palustris	0.25	5.85±2.86	6.10
Brackish Ponds & Streams			
Hippuris tetraphylla	0	0.05±0.05	0.05
Weedy			
Senecio congestis	0.25	10.25±3.85	10.50
Juncus bufonius	0	0.1±0.1	0.10
Other			
Unknown species 1	0	0.05±0.05	0.05
Total	296.00	38.05	334.05

Table 6. Percentage cover (±standard error) of species in vegetation of undamaged and degraded plots in an intertidal salt marsh on the eastern coast of La Pérouse Bay.

Species	Undamaged Sites (N=5)	Degraded Sites (N=5)	Species Total (frequency/200)
Salt Marsh Graminoid Sward			
Puccinellia phryganodes	92.30±2.50	9.20±3.97	101.50
Plantago maritima	3.90±3.31	1.00±1.00	4.90
Potentilla egedii	1.60±0.40	0.10±0.10	1.70
Carex subspathacea	1.00±0.88	0.90±0.78	1.90
Ranunculus cymbalaria	0.80±0.12	0	0.80
Stellaria humifusa	0.10±0.10	0	0.10
Hypersaline Mudflats			
Salicornia borealis	0.10±0.10	0	0.10
Spergularia marina	0.10±0.10	0	0.10
Brackish Marsh			
Triglochin palustris	0.30±0.20	0	0.30
Total	100.20	11.20	111.40

Table 7. Percentage cover (±standard error) of species in vegetation of undamaged and degraded plots in a supratidal salt marsh.

Species	Undamaged Sites		Degraded Sites		Species Total (frequency/ 400)
	Site 1 (N=5)	Site 2 (N=10)	Site 1 (N=5)	Site 2 (N=5)	
Salt Marsh Graminoid Sward					
Carex subspathacea	37.00±5.9	53.45±5.30	0.30±0.20	2.20±0.84	92.95
Puccinellia phryganodes	11.60±0.8	9.95±1.82	7.40±3.93	6.90±2.85	35.85
Potentilla egedii	10.20±4.0	7.35±1.06	0.10±0.10	0	17.65
Plantago maritima	2.50±1.0	0.15±0.08	0	0	2.65
Ranunculus cymbalaria	0.30±0.2	0.45±0.16	0	0	0.75
Dupontia fischeri	0	0.80±0.45	0	0	0.80
Salt Marsh Willow-Grassland					
Festuca rubra	8.00±2.4	13.25±3.93	0.20±0.20	0	21.45
Salix brachycarpa	0.40±0.2	0	0	0	0.40
Calamagrostis deschampsioides	0.10±0.1	1.30±0.35	0	0	1.40
Salix spp.	0.40±0.4	1.25±0.37	0	0	1.65
Parnassia palustris	0	0.25±0.20	0	0	0.25
Lomatogonium rotatum	0	0.20±0.08	0	0	0.20
Hypersaline Mudflats					
Salicornia borealis	0.40±0.5	0	0.10±0.10	0.10±0.10	0.90
Spergularia marina	0.10±0.1	0	0	0	0.10
Brackish Marsh					
Triglochin palustris	0	0.20±0.13	0	0	0.20
Euphrasia arctica	0	0.05±0.05	0	0	0.05
Weedy					
Juncus bufonius	0.30±0.2	0	0	0	0.30
Matricaria ambigua	0.10±0.1	0	0	0	0.10
Rumex occidentalis	0	0.10±0.07	0	0	0.10
Total	71.70	88.75	8.10	9.20	177.75

Table 8. Percentage cover of species in vegetation of undamaged and degraded plots in an inland salt marsh. The undamaged plots have been exclosed from goose grazing since 1985.

Species	Undamaged Sites (N=2)	Degraded Sites (N=2)	Species Total (frequency/200)
Salt Marsh Graminoid Sward			
Carex subspathacea	46.25	0	46.25
Puccinellia phryganodes	55.50	1.00	56.50
Potentilla egedii	20.75	0	20.75
Puccinellia nuttaliana	8.75	0	8.75
Ranunculus cymbalaria	5.25	0	5.25
Plantago maritima	1.00	0	1.00
Stellaria humifusa	1.00	0	1.00
Salt Marsh Willow-Grassland			
Festuca rubra	11.75	0	11.75
Lomatogonium rotatum	4.25	0	4.25
Parnassia palustris	0.25	0	0.25
Hypersaline Mudflats			
Salicornia borealis	0.75	32.50	33.25
Spergularia marina	0	0.75	0.75
Brackish Marsh			
Salix candida	1.25	0	1.25

Table 8 (cont.)

Species	Undamaged Sites (N=2)	Degraded Sites (N=2)	Species Total (frequency/200)
Euphrasia arctica	1.00	0	1.00
Salix planifolia	0.75	0	0.75
Weedy			
Senecio congestus	1.00	0	1.00
Achillea nigrescens	0.75	0	0.75
Other			
Unknown species 1	2.75	0	2.75
Total	163.00	34.25	197.25

Table 9. Percent cover (±standard error) of species in vegetation of undamaged and degraded plots on a beach ridge.

Species	Undamaged (N=6)	Degraded (N=6)	Species Total (frequency/200)
Salt Marsh Graminoid Sward			
Stellaria longipes	27.50±4.87	6.00±2.21	33.50
Ranunculus cymbalaria	7.08±1.80	5.92±1.55	13.00
Puccinellia phryganodes	0.08±0.08	1.25±0.81	1.33
Carex subspathacea	0	0.08±0.08	0.08
Dupontia fischeri	0	0.42±0.27	0.42
Puccinellia nuttaliana	0	0.08±0.08	0.08
Stellaria humifusa	0	0.17±0.17	0.17
Koenigia islandica	0	0.17±0.17	0.17
Salt Marsh Willow-Grassland			
Calamagrostis deschampsioides	11.91±4.86	3.42±1.92	15.33
Salix spp.	1.92±0.44	0.08±0.08	2.00
Lomatogonium rotatum	1.92±0.98	0.17±0.17	2.08
Festuca rubra	0.50±0.26	0.42±0.20	0.92
Senecio pauperculus	0.42±0.33	0.08±0.08	0.50
Rhinanthus borealis	0.17±0.17	0	0.17
Salix brachycarpa	0.08±0.08	0.25±0.17	0.33
Hypersaline Mudflats			
Atriplex patula	0.67±0.21	5.08±3.40	5.75
Spergularia marina	0.08±0.08	0	0.08
Brackish Marsh			
Triglochin palustris	0.08±0.08	0	0.08
Euphrasia arctica	0.17±0.17	0	0.17
Beach Ridge			
Leymus mollis	72.58±9.76	0	72.58
Potentilla norvegica	3.33±1.74	0.50±0.41	3.83
Minuartia rubella	1.25±1.25	1.50±0.60	2.75
Hordeum jubatum	0.42±0.42	0.17±0.17	0.58
Weedy			
Matricaria ambigua	23.50±5.36	68.67±5.62	92.17
Senecio congestus	4.08±1.12	0.92±0.40	5.00
Rumex occidentalis	0.33±0.25	0.08±0.08	0.42
Achillea nigrescens	0.25±0.17	0	0.25
Other			
Unknown species 1	0.25±0.17	1.34±0.95	1.58
Total	158.58	96.8	255.33

Figure 10. Relative abundance of assemblages of plant species in different coastal habitats at La Pérouse Bay, Manitoba, found in the above ground vegetation a) where vegetation is undamaged and b) where soil is degraded. To examine the species composition of each assemblage type, consult Tables 5-9.

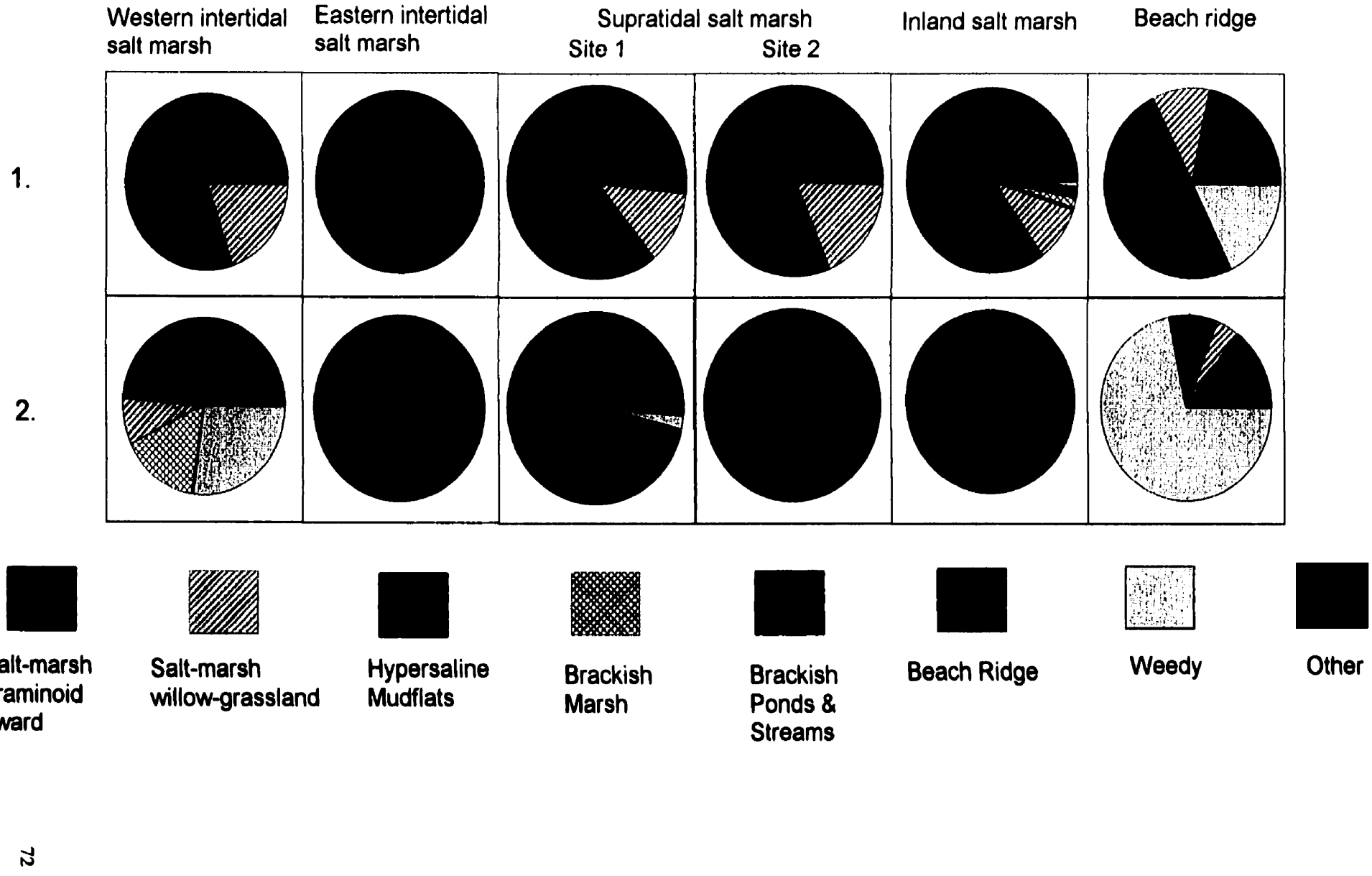
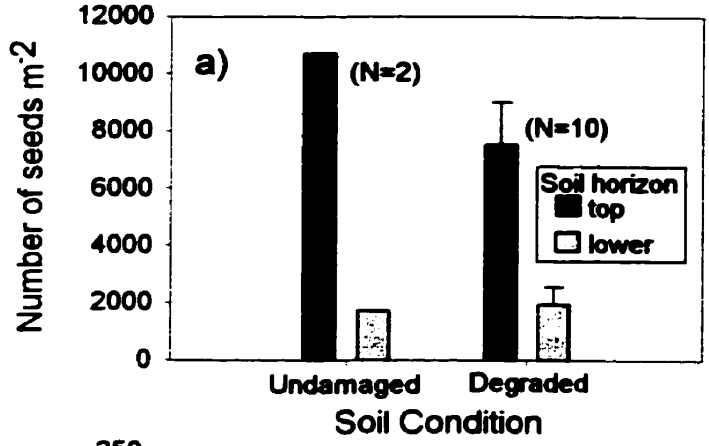
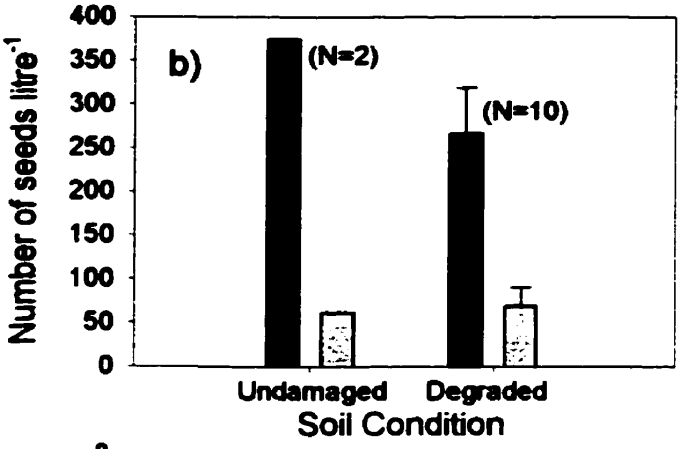
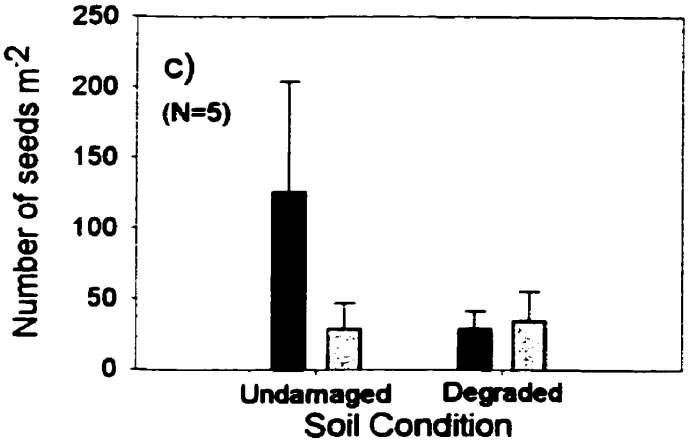
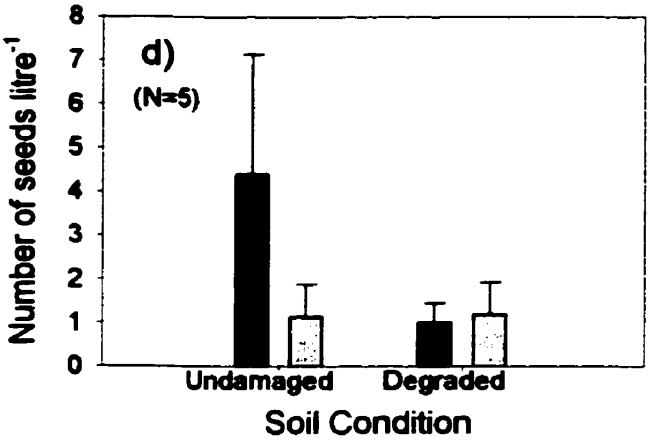

Western intertidal salt marsh
Eastern intertidal salt marsh
Supratidal salt marsh
Site 1
Site 2
Inland salt marsh
Beach ridge
1.
2.
Salt-marsh graminoid sward
Salt-marsh willow-grassland
Hypersaline Mudflats
Brackish Marsh
Brackish Ponds & Streams
Beach Ridge
Weedy
Other

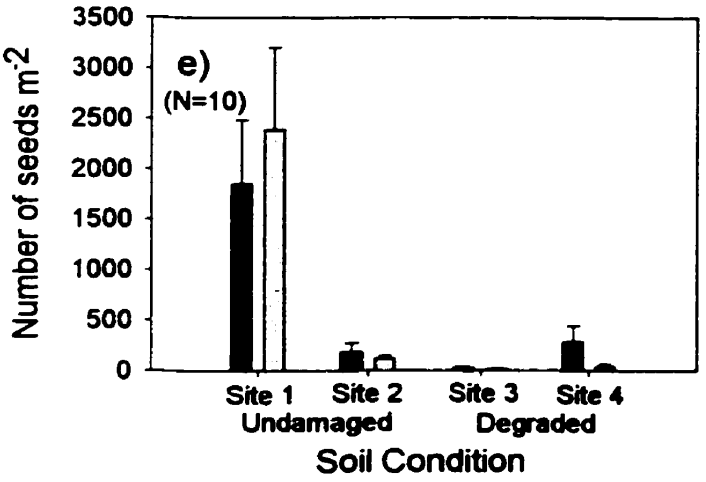
Figure 11. Seed bank density (all species pooled) of undamaged and degraded salt-marsh sites expressed per unit area and per unit volume. (a) & (b) western intertidal plots at La Pérouse Bay; Wilcoxon rank-sum test was used to test for effects of soil degradation (n.s.), soil depth ($p<0.001$) and degradation-depth interaction (n.s.), (c) & (d) eastern intertidal salt-marsh plots; Wilcoxon rank-sum test was used to test for effects of soil degradation (n.s.), soil depth (n.s.) and degradation-depth interaction (n.s.), (e) & (f) supratidal marsh; general linear model using poisson distribution showed significant differences between undamaged plots and plots where the soil was damaged ($p<<0.001$) and sites ($p<0.001$), (g) & (h) inland marsh; range is given for upper and lower layers of soil in exclosed plots, and upper and lower layers of soil in damaged plots respectively: 800-3400 seeds m^{-2}, 86-110 seeds m^{-2}, 940-2200 seeds m^{-2} and 260-285 seeds m^{-2}. Density was originally calculated per unit volume due to the unequal sampling of depth and then converted into the less accurate per unit area. Sample sizes are contained in parentheses. Note that the western intertidal salt-marsh has uneven sample sizes. Soil samples beneath undamaged vegetation for the western intertidal and inland salt-marsh came from exclosures that had been erected to exclude geese in 1982 and 1984 respectively. Consult legend in (a) for explanation of soil layers.

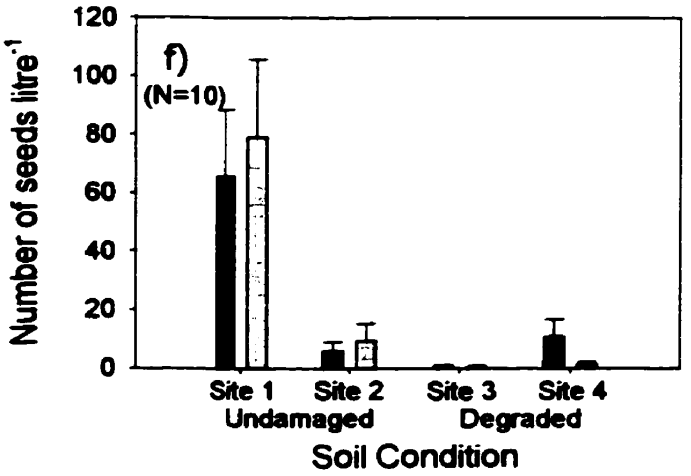

a)
(N=2)
(N=10)
Soil horizon
top
lower
Number of seeds m-2
12000
10000
8000
6000
4000
2000
0
Undamaged
Degraded
Soil Condition

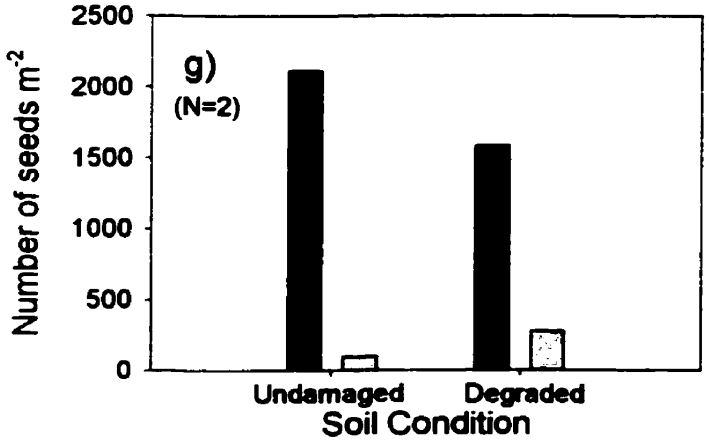

b)
(N=2)
(N=10)
Number of seeds litre-1
400
350
300
250
200
150
100
50
0
Undamaged
Degraded
Soil Condition

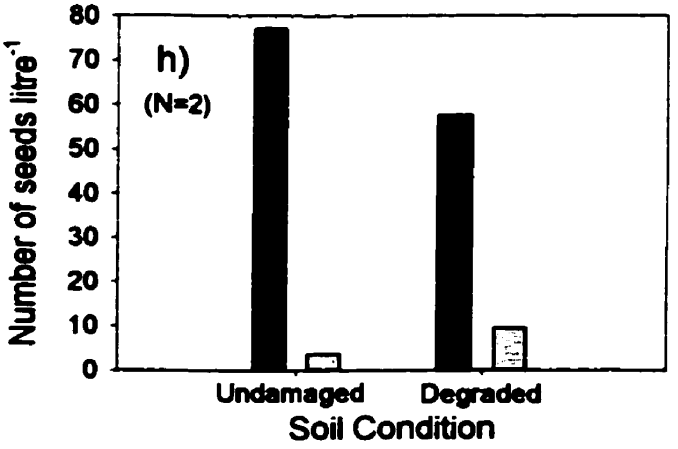

c)
(N=5)
Number of seeds m-2
250
200
150
100
50
0
Undamaged
Degraded
Soil Condition


d)
(N=5)
Number of seeds litre-1
8
7
6
5
4
3
2
1
0
Undamaged
Degraded
Soil Condition


e)
(N=10)
Number of seeds m-2
3500
3000
2500
2000
1500
1000
500
0
Site 1
Site 2
Site 3
Site 4
Undamaged
Degraded
Soil Condition


f)
(N=10)
Number of seeds litre-1
120
100
80
60
40
20
0
Site 1
Site 2
Site 3
Site 4
Undamaged
Degraded
Soil Condition


g)
(N=2)
Number of seeds m-2
2500
2000
1500
1000
500
0
Undamaged
Degraded
Soil Condition


h)
(N=2)
Number of seeds litre-1
80
70
60
50
40
30
20
10
0
Undamaged
Degraded
Soil Condition

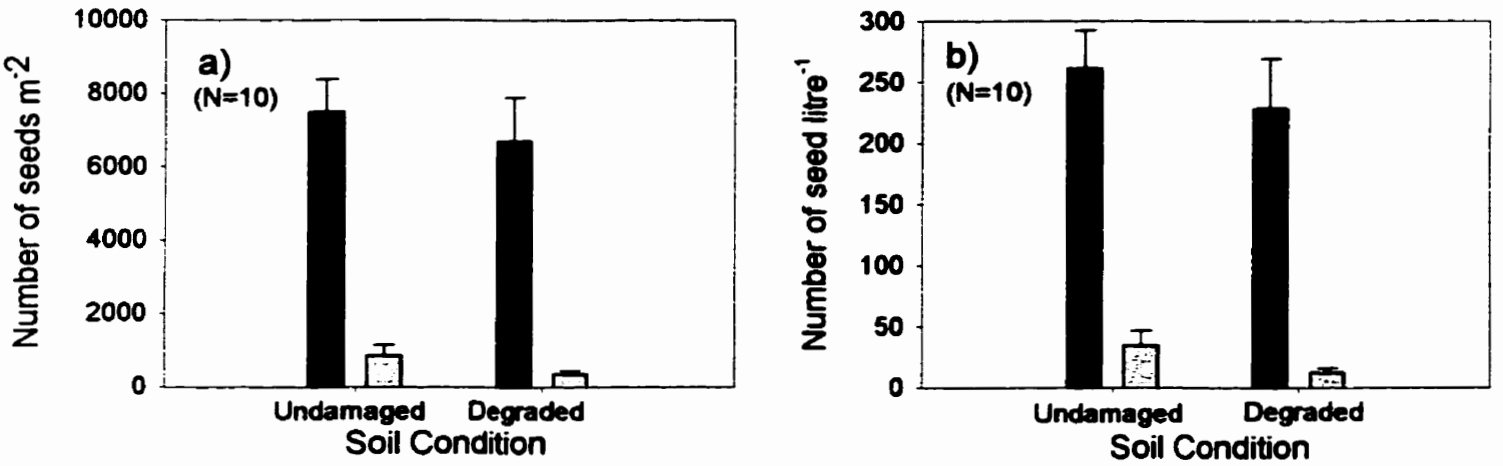


Figure 12. Seed bank density (all species pooled) of undamaged and degraded beach-ridge plots expressed per unit area (a) and per unit volume (b). Wilcoxon rank-sum test used to test for soil degradation (n.s.), soil layer ($p < 0.001$) and degradation-layer interaction effects (n.s.). Consult legend in Fig. 11 (a) for explanation of soil layers.

However, there were clear differences in the abundance of seeds with soil depth in the different plots (Wilcoxon rank-sum test, n=10, m=10, W_n=59, p<0.001 for intertidal marsh on western coast of Bay; n=10, m=10, W_n=55, p<0.001 for beach ridge). Overall, three times to ten times more seeds were found in the upper section of soil compared to values for the lower section at a greater depth. In the plots in the eastern intertidal marsh (Fig. 11c, d), there were no consistent differences in seed densities in relation to soil depth (Wilcoxon rank-sum test, n=5, m=5, W_n=23.5, n.s.) or between undamaged and damaged plots (Wilcoxon rank-sum test, n=5, m=5, W_n=22.5, n.s.). In the supratidal marsh, the seed bank found in undamaged plots was greater than that found in degraded plots (general linear model, df=1, F=17.856, p<<0.001). There were also significant differences in the soil seed bank sampled at different sites in the supratidal marsh (general linear model, df=1, F=7.1, p<0.001).

Overall, twenty-three species in total were found in the seed banks of which very few were monocotyledonous species. These species were assigned to the assemblage group that they were most closely associated with in the above-ground vegetation (Tables 10-14). *R. cymbalaria*, a buttercup with small achenes around 1.2mm in length represented the graminoid swards characteristic of salt-marsh vegetation. Seeds of *Salicornia borealis*, an annual tolerant of high salinity, were an indicator of hypersaline mudflat sediments. Species characteristic of brackish marsh, brackish ponds and streams, and freshwater ponds and streams, which occur geographically close to the sampled salt marsh plots, were also found in the seed bank suggesting that some seeds dispersed in the plots were incorporated into the seed bank. The weedy assemblage consisted of mostly ruderal species that colonize disturbed soils but are not highly salt tolerant. The most

Table 10. Density of species found in seed bank (seeds m^{-2} ± s.e.) of intertidal salt marsh on western coast of La Pérouse Bay. * each sample contains 10 pooled soil cores. + range from minimum to maximum thickness. ++ thickness of layer. Seed bank persistence data classified according to Thompson *et al.* 1997 (Fig. 2) given in species column: T=transient, SP=short-term persistence, LP=long-term persistence.

Species	Undamaged (N=2* for each layer)		Degraded (N=10* for each layer)		Species Total (seeds/4m²)
	Top layer (3cm)++	Lower layer (2.5-3cm)+	Top layer (2.2-3.0cm)+	Lower layer (2.5-3.0cm)+	
Salt Marsh Graminoid Sward					
Ranunculus cymbalaria (SP)	9380	471	7100±1500	1900±594	18860
Carex subspathacea (T)	343	0	2.86±2.86	0	346
Potentilla egedii (T)	257	0	5.71±5.71	2.86±2.86	266
Salt Marsh Willow-Grassland					
Festuca rubra (T)	85.7	0	5.71±2.81	5.71±3.81	97.1
Salix spp.	14.3	28.6	11.4±6.32	8.57±7.18	62.8
Hypersaline Mudflats					
Salicornia borealis (T)	28.6	0	0	2.86±2.86	31.4
Spergularia marina	14.3	0	0	0	14.3
Atriplex patula	0	14.3	0	0	14.3
Brackish Ponds & Streams					
Hippuris spp. (LP)	171	1160	266±83.5	22.8±14.0	1620
Weedy					
Senecio congestus (SP)	314	71.4	5.71±3.81	0	391
Stellaria longipes	71.4	0	2.86±2.86	0	74.3
Juncus bufonius	0	0	51.4±38.3	0	51.4
Matricaria ambigua	14.3	0	0	2.86±2.86	17.1
Achillea nigrescens	0	0	2.86±2.86	0	2.86
Other					
Unknown Species 1	0	0	68.6±53.06	14.3±7.68	82.8
Total	10700	1740	7520±1480	1960±607	21920

Table 11. Density of species found in seed bank (seeds m^{-2} ±s.e.) of intertidal salt marsh on eastern coast of La Pérouse Bay. * each sample contains 10 pooled soil cores. + range from minimum to maximum thickness. ++ thickness of layer. Seed bank persistence data given in species column: T=transient, SP=short-term persistence, LP=long-term persistence.

Species	Undamaged (N=5 for each layer)*		Degraded (N=5 for each layer)*		Species Total (seeds/4m²)
	Top layer (3.0cm)++	Lower layer (2.0-3.0cm)+	Top layer (3.0cm)++	Lower layer (2.5-3.0cm)+	
Salt Marsh Graminoid Sward					
Ranunculus cymbalaria (SP)	120±80.0	0	17.1±11.4	0	137
Salt Marsh Willow-Grassland					
Salix spp.	0	17.1±11.4	5.71±5.71	22.8±16.6	45.7
Festuca rubra	0	5.71±5.71	0	0	5.71
Brackish Ponds & Streams					
Hippuris spp.	5.71±5.71	0	5.71±5.71	11.4±7.00	22.8
Weedy					
Senecio congestus	0	5.71±5.71	0	0	5.71
Total	126±78.0	28.6±18.1	28.6±12.8	34.3±21.0	217

Table 12. Density of species found in seed bank (seeds m^{-2} ±s.e.) of supratidal salt marsh. * each sample contains 10 pooled soil cores. + range from minimum to maximum thickness. Seed bank persistence data given in species column: T=transient, SP=short-term persistence, LP=long-term persistence.

Species	Undamaged (N=10* for each layer)				Degraded (N=10* for each layer)				Species Total (seeds/8m²)
	Site 1		Site 2		Site 3		Site 4		
	Organic layer (2.1-3.5cm)+	Mineral layer (2.0-3.5cm)+	Organic layer (2.3-3.7cm)+	Mineral layer (2.0-3.5cm)+	Top layer (2.0-4.5cm)+	Lower layer (1.5-4.6cm)+	Top layer (1.6-3.7cm)+	Lower layer (1.6-3.4cm)+	
Salt Marsh Graminoid Sward									
Ranunculus cymbalaria (LP)	948±425	1820±772	134±89.2	97.1±24.5	0	0	11.42±6.32	8.57±4.36	3020
Potentilla egedii (SP)	17.1±6.32	0	2.86±2.86	11.43±8.73	0	0	0	0	31.4
Stellaria longipes	0	5.71±3.81	2.86±2.86	0	1.43±1.43	0	5.71±3.81	0	15.71
Salt Marsh Willow-Grassland									
Salix spp. (T)	68.6±17.1	5.71±3.81	14.3±7.68	0	0	0	17.1±12.2	0	105.7
Festuca rubra (SP)	14.3±7.68	8.57±6.10	5.71±5.71	0	0	0	0	0	28.6
Primula spp.	0	0	2.86±2.86	0	0	0	0	0	2.86
Hypersaline Mudflats									
Salicornia borealis (T)	54.3±20.6	0	8.57±4.36	2.86±2.86	8.57±6.10	11.4±11.4	234±139	22.86±22.86	343
Spergularia marina	0	0	0	0	0	0	2.86±2.86	2.86±2.86	5.71
Brackish Ponds and Streams									
Hippuris spp. (LP)	37.1±17.1	91.4±53.0	0	8.57±6.10	0	0	0	2.86±2.86	140.0
Ranunculus gmelini ssp. *purshii*	0	2.86±2.02	0	0	0	0	0	0	2.86
Freshwater Ponds and Streams									
Carex aquatilis	0	0	5.71±3.81	0	0	0	0	0	5.71
Weedy									
Juncus bufonius (LP)	694±534	434±369	0	0	0	0	0	0	1128
Senecio congestus	8.57±4.36	17.1±11.4	0	0	2.86±2.86	0	0	0	28.6
Achillea nigrescens	0	0	0	0	0	0	8.57±8.57	0	8.57
Matricaria ambigua	0	0	0	0	2.86±2.86	0	0	0	2.86
Other									
Rosaceae (LP)	0	5.71±5.71	8.57±6.10	0	7.14±3.84	0	0	0	21.43
Unknown species 1	0	0	0	0	1.43±1.43	0	0	0	1.43
Total	1843±637	2390±810	186±90	120.0±25.5	24.28±6.04	11.4±11.4	280±157	37.14±25.22	4896

Table 13. Density of species found in seed bank (seeds m^{-2}) of inland salt-marsh. * each sample contains 10 pooled soil cores. + range from minimum to maximum thickness. ++ thickness of layer.

Species	Undamaged (N=2* for each layer)		Degraded (N=2* for each layer)		Species Total (seeds/4m^2)
	Organic layer (2.4-3.0cm)+	Mineral layer (2.0-3.0cm)+	Organic layer (2.5-3.5cm)+	Mineral layer (3.0cm)++	
Salt Marsh Graminoid Sward					
Ranunculus cymbalaria	28.6	28.6	42.8	0	100.0
Salt Marsh Willow-Grassland					
Salix spp.	14.3	0	42.8	28.6	85.7
Festuca rubra	0	0	14.3	0	14.3
Hypersaline Mudflats					
Salicornia borealis	2040	14.3	943	243	3243
Spergularia marina	14.3	0	14.3	0	28.6
Atriplex patula	14.3	0	42.8	0	57.1
Brackish Marsh					
Triglochin palustris	0	14.3	0	0	14.3
Brackish Ponds & Streams					
Hippuris spp.	0	0	14.3	0	14.3
Weedy					
Juncus bufonius	0	28.6	443	0	471
Senecio congestus	0	14.3	28.6	0	42.8
Total	2114	100.0	1586	271	4071

Table 14. Density of species found in seed bank (seeds m^{-2} ± s.e.) of beach ridge. • each sample contains 10 pooled species. + range from minimum to maximum thickness. Seed bank persistence data given in species column: T=transient, SP=short-term persistence, LP=long-term persistence.

Species	Undamaged (N=10 for each layer)*		Degraded (N=10 for each layer)*		Species Total (seeds/4m^2)
	Organic layer (2.5-4.0cm)+	Mineral layer (1.0-3.5cm)+	Organic layer (2.5-4.5cm)+	Mineral layer (1.5-4.0cm)+	
Salt Marsh Graminoid Sward					
Ranunculus cymbalaria (SP)	1960±631	137±74.3	471±150	34.3±10.2	2600
Stellaria longipes (SP)	237±82.1	20.0±8.57	42.8±14.3	14.3±8.78	314
Potentilla egedii	2.86±2.86	0	0	0	2.86
Salt Marsh Willow-Grassland					
Festuca rubra (SP)	468±186	208±130	8.57±6.10	2.86±2.86	688
Carex subspathacea	0	22.8±22.8	0	0	22.8
Salix spp.	2.86±2.86	8.57±6.10	5.71±3.81	2.86±2.86	20.00
Senecio pauperculus	0	2.86±2.86	0	0	2.86
Hypersaline Mudflats					
Atriplex patula (SP)	843±444	74.3±58.9	1010±753	8.57±6.10	1940
Spergularia marina (SP)	42.8±28.3	5.71±5.71	137±131	2.86±2.86	188
Salicornia borealis	2.86±2.86	0	0	0	2.86
Brackish Ponds & Streams					
Hippuris spp.	0	0	2.86±2.86	0	2.86
Beach Ridges					
Saxifraga oppositifolia	0	0	0	2.86±2.86	2.86
Weedy					
Matricaria ambigua (SP)	2880±633	234±107	4570±1040	203±67.4	7890
Senecio congestus (SP)	951±152	131±44.5	388±85.1	60.0±53.8	1531
Juncus bufonius	0	2.86±2.86	42.8±34.4	2.86±2.86	48.6
Achillea nigrescens	0	0	2.86±2.86	0	2.86

Table 14 (cont.)

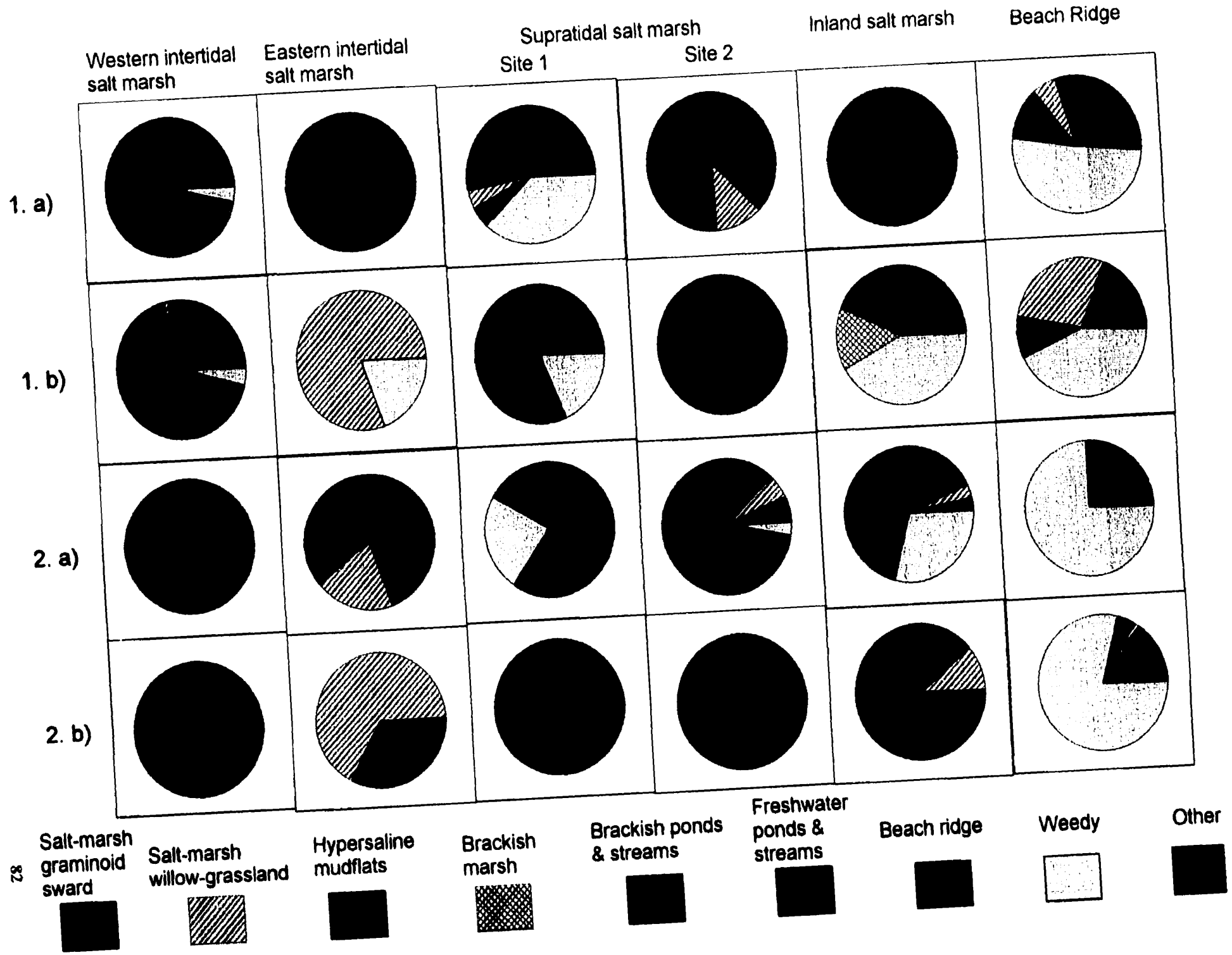
Species	Undamaged (N=10 for each layer)•		Degraded (N=10 for each layer)*		Species Total (seeds/4m²)
	Organic layer (2.5-4.0cm)+	Mineral layer (1.0-3.5cm)+	Organic layer (2.5-4.5cm)+	Mineral layer (1.5-4.0cm)+	
Other					
Unknown Species 1	106±41.7	5.71±35.6	11.4±4.67	0	123
Total	7490±886	854±286	6700±1190	334±96.9	15380

widespread species of this assemblage type in the seed bank was *Juncus bufonius*, a widely distributed annual species with many records indicating a persistent seed bank (Thompson *et al.* 1997). Only four species appeared to be members of long-term persistent seed banks in this study: *Ranunculus cymbalaria*, *Hippuris* spp., *Juncus bufonius* and an unidentified member of Rosaceae that is not found in the La Pérouse Bay flora at present (Tables 10-14). It should be noted that all of the dominant species in the vegetation (*Puccinellia phryganodes* and *Carex subspathacea* in the salt marsh, *Leymus mollis* on the beach ridge) either possess very extremely small seed banks or do not form seed banks at all.

The soil seed banks of plots in the supratidal marsh and on the beach ridge showed shifts in relative abundance of seeds of different species in response to soil degradation comparable to changes in the vegetation (Fig. 13). Changes in the soil seed bank from undamaged plots to plots where the soil was degraded were characterized by fewer supratidal species, beach ridge species and more ruderal species. These changes were more evident in the supratidal plots than in plots on the beach ridge.

In contrast, the seed banks in the western intertidal and inland salt marshes showed little change in the overall species assemblage from plots where the vegetation was undamaged to plots where the soil was degraded (Fig. 13). Species typical of the salt-marsh graminoid sward dominated the composition of the seed bank in the western

Figure 13. Relative abundance of plant assemblages found in the soil seed bank. 1. undamaged soils, 2. degraded soils, (a) organic or top layer of soil, (b) mineral or lower layer of soil. The presence of an organic layer depends upon the salt-marsh zonation and the site condition. To see species composition of each assemblage type, consult Tables 10-14.


Western intertidal salt marsh
Eastern intertidal salt marsh
Supratidal salt marsh
Site 1
Site 2
Inland salt marsh
Beach Ridge
1. a)
1. b)
2. a)
2. b)
Salt-marsh graminoid sward
Salt-marsh willow-grassland
Hypersaline mudflats
Brackish marsh
Brackish ponds & streams
Freshwater ponds & streams
Beach ridge
Weedy
Other

intertidal marsh, except in the lower layers of the soil in plots where the vegetation was undamaged. The assemblage typical of brackish ponds and streams consisted mostly of *Hippuris* spp. and this assemblage formed 67% of the soil seed bank in the lower layers of soils in plots where undamaged salt-marsh vegetation occurred in the western intertidal marsh. Seeds representative of plants growing in the hypersaline mud flats, the vegetation typical of degraded salt marshes, had the greatest relative abundance in plots at the inland salt marsh. They made up most of the seed bank of plots where soil was degraded (60% and 90% at this location), as well as that in the upper organic layers of plots where undamaged vegetation grew (97%). The weedy assemblage formed a significant proportion of the seed bank in the mineral layers of plots where the vegetation was undamaged and in the organic layers of plots where soil was degraded.

The soil seed density was so low in the eastern intertidal sites at La Pérouse Bay that it was difficult to assess the affinities of seeds to plant assemblages. The only species to have a density of at least 100 seeds m^{-2} was *R. cymbalaria*, which was in the top layer of the soil at plots where the vegetation was undamaged.

3.3.3 Vegetation ordination constrained by seed bank

Overall, the eight seed bank variables (PCA axes one to eight) and three soil variables (salinity and percentages of soil that were silt and sand) explained 44.4% ($p<0.005$) of the variation in the species data (Table 15). The first two axes collectively contained 35.7% and the first three axes accounted for 42.0 % of the variability. Tests on both the first axis and the total configuration showed a high level of significance ($p<0.005$). For the eight modified seed bank variables, the first eight PCA axes explained 89% of the seed

Table 15. Components of Variance for RDA. Vegetation data were constrained by seed bank data. *significance at $p<0.05$ and **significance at $p<0.005$ using Monte Carlo random simulation.

Source of Variation	Including Interaction Terms	Unique Contribution
Seed bank	31.9%**	16.6%*
Soil	27.8%**	12.5%**
Seed bank x Soil Interaction	15.3%	
Explained	44.4%**	
Error	55.6%	
Total	100%	

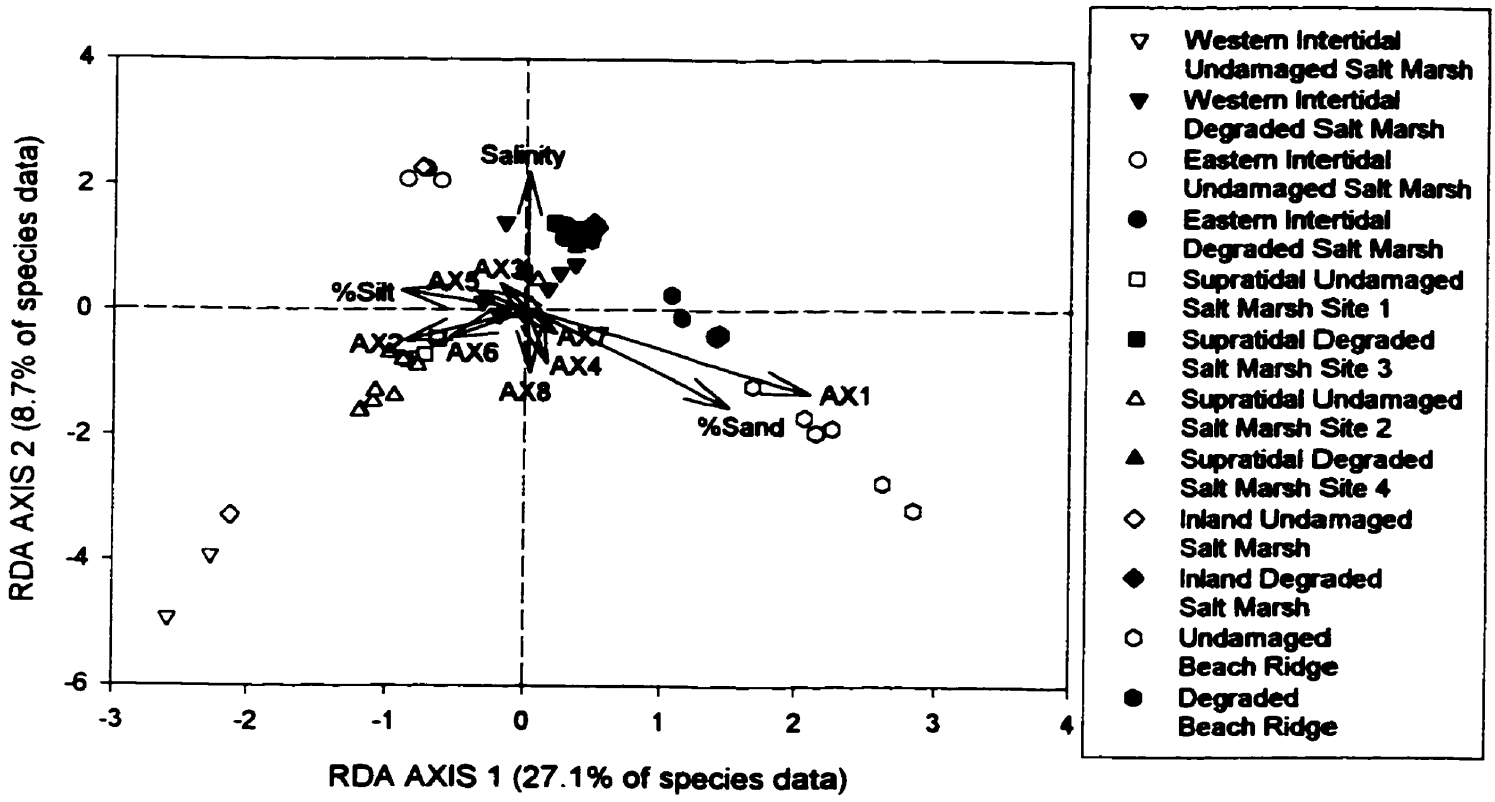
Note: CANOCO does not allow for a test of significance of the seed bank x soil interaction factor.

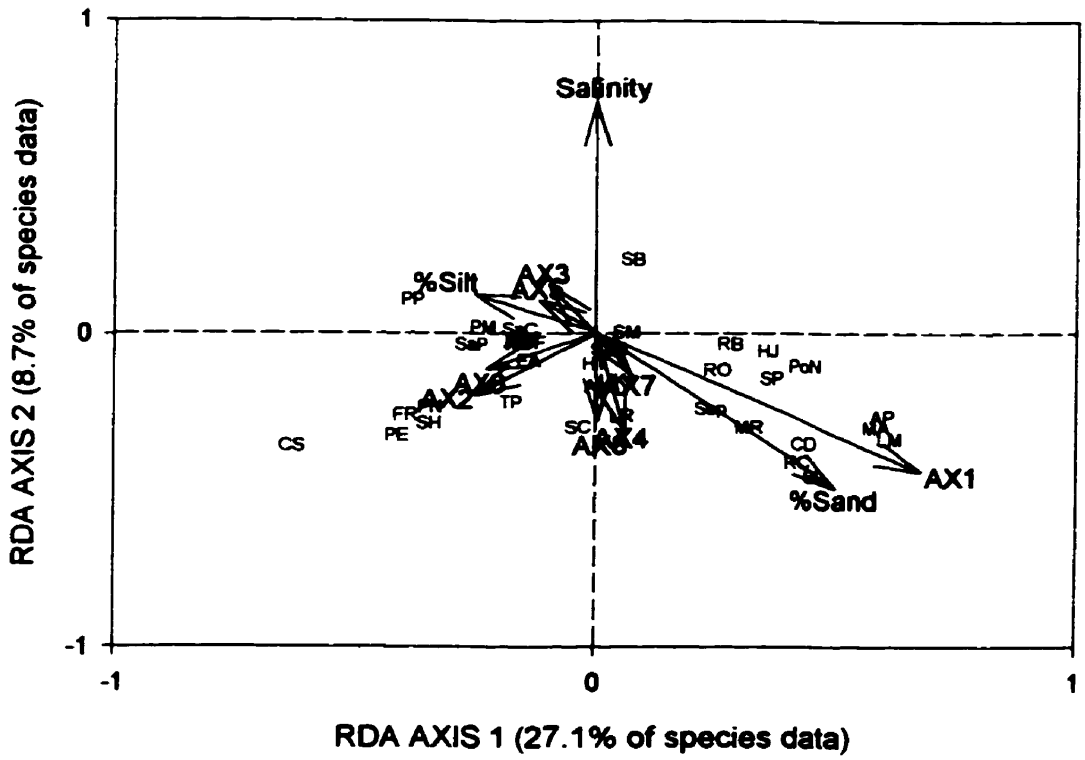
bank variance with 56.7% contained within the first two axes. The first RDA axis separated the salt-marsh plots with more silt in their soil from the sandier beach ridge plots, as shown in the sample-variable biplot (Fig. 14a). The first PCA axis followed by percentage of sand and percentage of silt in the particle size distribution possess the highest correlations with this axis. The species loadings of the first PCA axis of the seed bank data show that beach-ridge plots tend to have more seeds of *Atriplex patula*, *Matricaria ambigua*, *Senecio congestus* and *Stellaria longipes* present in the soil while more *Carex aquatilis*, *Hippuris* spp. and *Salicornia borealis* seeds tend to be found under salt-marsh plots (Table 16). The second RDA axis represented a disturbance gradient with salinity (sodium concentration) showing the highest correlation to this axis. Proportion of sand in the soil was also an important environmental factor. The placement of plots along the disturbance gradient corresponded well with *a priori* assignment. In the salt marshes, three of the long-term exclosures were at one extreme with all of the plots containing the degraded soils at the other extreme. Supratidal plots where the vegetation was undamaged were intermediate. The eastern intertidal plots where

Table 16. Species loadings of the seed bank PCA. These first eight axes were used as constraining variables in the vegetation RDA (Fig. 14 & 15). The species abbreviations are symbols used in species-variable biplots.

Species Name (including abbreviations)		AX1	AX2	AX3	AX4	AX5	AX6	AX7	AX8
Achillea nigrescens	AN	.0413	.2251	-.1184	-.0972	-.0764	-.1619	.1151	-.2062
Atriplex patula	AP	**.9191**	-.2473	.0983	.0562	.0292	.0107	.1536	.1121
Carex aquatilis	CA	**-.1383**	.0555	-.0358	-.1093	-.0348	-.0054	.2049	.0778
Carex subspathacea	CS	.2670	.4127	.1012	-.3543	-.1032	-.3098	-.0128	-.1358
Festuca rubra	FR	.5970	.3714	.1714	-.3319	.1366	-.0521	-.4956	-.1232
Hippuris spp.	Hsp	**-.1402**	.8143	-.1356	-.2459	.2306	-.2162	.3268	.0968
Juncus bufonius	JB	-.0899	.3032	.4381	.6000	.4467	-.0636	-.0677	-.2423
Matricaria ambigua	MA	**.9428**	-.2040	-.1405	.0380	.0105	.0299	.0603	.0380
Potentilla egedii	PE	-.0144	.4842	.2326	-.4837	-.2967	-.1636	.1160	-.1567
Primula spp.	Psp	-.0872	.0205	.1060	-.0492	-.1632	.2048	.0140	.0688
Ranunculus cymbalaria	RC	.3913	.7785	-.1234	.3299	-.3119	.1216	-.0142	-.0158
Salicornia borealis	SB	**-.1570**	-.0163	.8890	.0267	-.2909	-.1687	-.0063	.2228
Salix lanata	SaL	-.0876	.0828	.2707	.3650	.1736	.2362	-.0901	-.1245
Salix spp.	Ssp	.0371	.4099	.3686	-.2563	.2890	.7019	.0470	.1841
Saxifraga oppositifolia	SO	.1960	-.1548	-.1253	.0241	.0376	-.0746	.0479	.0979
Spergularia marina	SM	.5429	-.0991	.3215	.1345	.0478	-.0320	.2837	.1378
Senecio congestus	SC	**.9104**	.0041	.2011	-.0398	.1006	-.1089	.1142	-.1876
Stellaria longipes	SL	**.7836**	-.0035	-.0381	-.2877	-.1904	.1071	-.1537	.0021
Triglochin palustris	TP	-.0264	-.1087	.2758	.0494	-.2141	-.1725	.0709	.1464
Rosaceae	ROS	**-.1670**	.0383	.0837	-.1756	.1083	.1369	.0931	-.0493
Unknown Species 1	UK1	.4176	.2688	-.2405	.1912	.2706	-.3182	-.3605	.5466

Figure 14. Redundancy analysis (RDA) based upon percentage cover of species in the vegetation constrained by density of species in the soil seed bank and three soil variables. Seed bank data were transformed using $y = \log (x + 1)$. AX1 to AX8 are axes resulting from principal component analysis (PCA) of the soil seed bank data which summarize trends seen in the data. (a) sample-variable biplot; arrows representing the constraining variables were magnified three times. (b) species-variable biplot; note difference in scaling from (a), as constraining variable arrows were not magnified. Symbols representing different plots are explained in the inset legend. A key to the species abbreviations is given in Table 16.


RDA AXIS 2 (8.7% of species data)
RDA AXIS 1 (27.1% of species data)
Salinity
%Silt
%Sand
AX1
AX2
AX3
AX4
AX5
AX6
AX7
AX8
Western Intertidal Undamaged Salt Marsh
Western Intertidal Degraded Salt Marsh
Eastern Intertidal Undamaged Salt Marsh
Eastern Intertidal Degraded Salt Marsh
Supratidal Undamaged Salt Marsh Site 1
Supratidal Degraded Salt Marsh Site 3
Supratidal Undamaged Salt Marsh Site 2
Supratidal Degraded Salt Marsh Site 4
Inland Undamaged Salt Marsh
Inland Degraded Salt Marsh
Undamaged Beach Ridge
Degraded Beach Ridge


RDA AXIS 2 (8.7% of species data)
RDA AXIS 1 (27.1% of species data)
Salinity
%Silt
%Sand
AX1
AX2
AX3
AX4
AX5
AX6
AX7
SB
RB
HJ
RO
SP
PoN
MR
CD
AP
LM
CS
PE
SH
TP

vegetation was intact and one of the inland exclosures formed a group on the third axis (Fig. 15). These plots have moderately high plant cover but low species diversity, which suggests partial damage or recent colonization and development of a graminoid sward. A herd of caribou trampled and grazed the vegetation of the inland exclosure in 1994 and 1996. Competitive exclusion is unlikely to account for the vegetation patterns in these plots as this process usually occurs in higher successional willow-grassland sites covered with swards of *Festuca rubra* and *Calamagrostis deschampsioides* rather than grazed *Puccinellia-Carex* swards.

Using bipartial canonical ordination, the unique contribution of the soil seed bank in explaining vegetation variance (16.6%; $p<0.05$) was found to be slightly larger than the unique contribution of the soil variables (12.5%; $p<0.005$) (Table 15). Their relatively large interaction factor (15.3%) was expected, as the floristic data should incorporate these two components.

The species-variable biplot (Fig. 14b) shows the distribution of the species that contribute to the vegetation. Species are tightly distributed according to the level of disturbance and their association with the salt marshes or the beach ridge.

3.3.4 Seed bank ordination constrained by vegetation

The modified vegetation and soil variables were better predictors of the soil seed bank than vice-versa explaining 52.5% ($p<0.005$) of the variance (Table 17). The first two axes collectively accounted for 37.8% of the variability. The vegetation PCA was slightly more successful than the seed bank PCA with the first eight axes explaining 97.6% of the variance in the vegetation. As in the constrained vegetation ordination, the

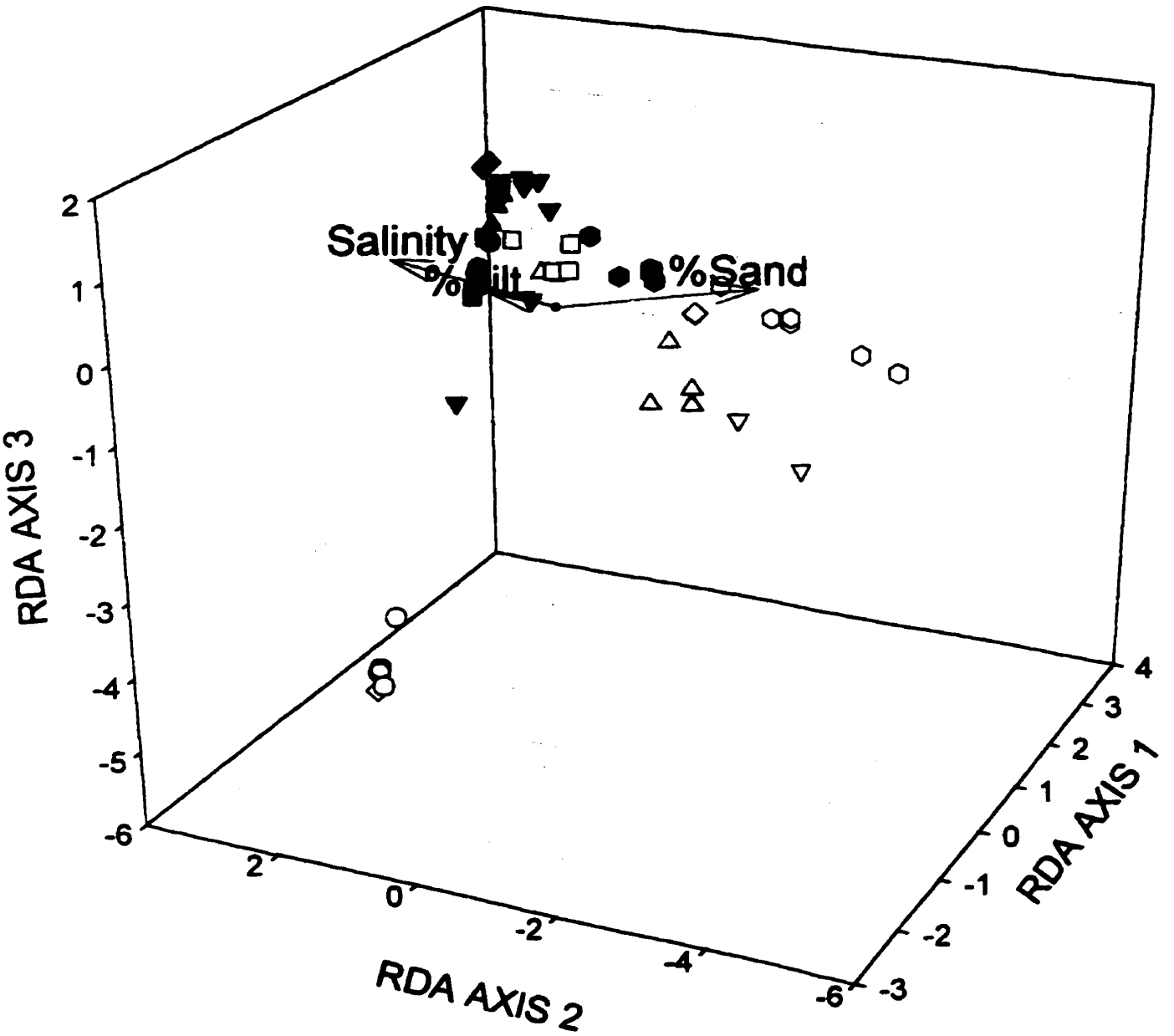


Figure 15. Three-dimensional version of RDA sample-variable biplot given in Fig. 14 (a).

Table 17. Components of Variance for RDA. Seed bank data were constrained by vegetation data. **significance at $p<0.005$ using Monte Carlo random simulation.

Source of Variation	Including Interaction Terms	Unique Contribution
Vegetation	41.8%**	26.5%**
Soil	26.0%**	10.7%**
Vegetation x Soil Interaction	15.3%	
Explained	52.5%**	
Error	47.5%	
Total	100%	

Note: CANOCO does not allow for a test of significance of the seed bank x soil interaction factor.

first RDA axis separated the salt-marsh plots from the beach-ridge plots based upon soil texture (Fig. 16a). The fourth PCA axis, percentage of sand and percentage of silt in the particle size distribution had the highest correlations with this axis. Salinity was also influential as salt-marsh soils were generally more saline than beach-ridge soils. Similarly, the second RDA axis represented a disturbance gradient with salinity and the sixth PCA axis having the highest correlations with this axis among the canonical variables. The species loadings for the PCA of the vegetation data are given in Table 18 but it is not clear what environmental gradients axes four and six represent. The seed bank ordination, however, differed in some aspects from the vegetation ordination. Most notably, the degraded western intertidal plots at La Pérouse Bay had a seed bank composition characteristic of "undamaged" vegetation while the two exclosures in the inland marsh had seed banks typical of degraded soils. The species-variable biplot again shows a tight scatter around the origin (Fig. 16b).

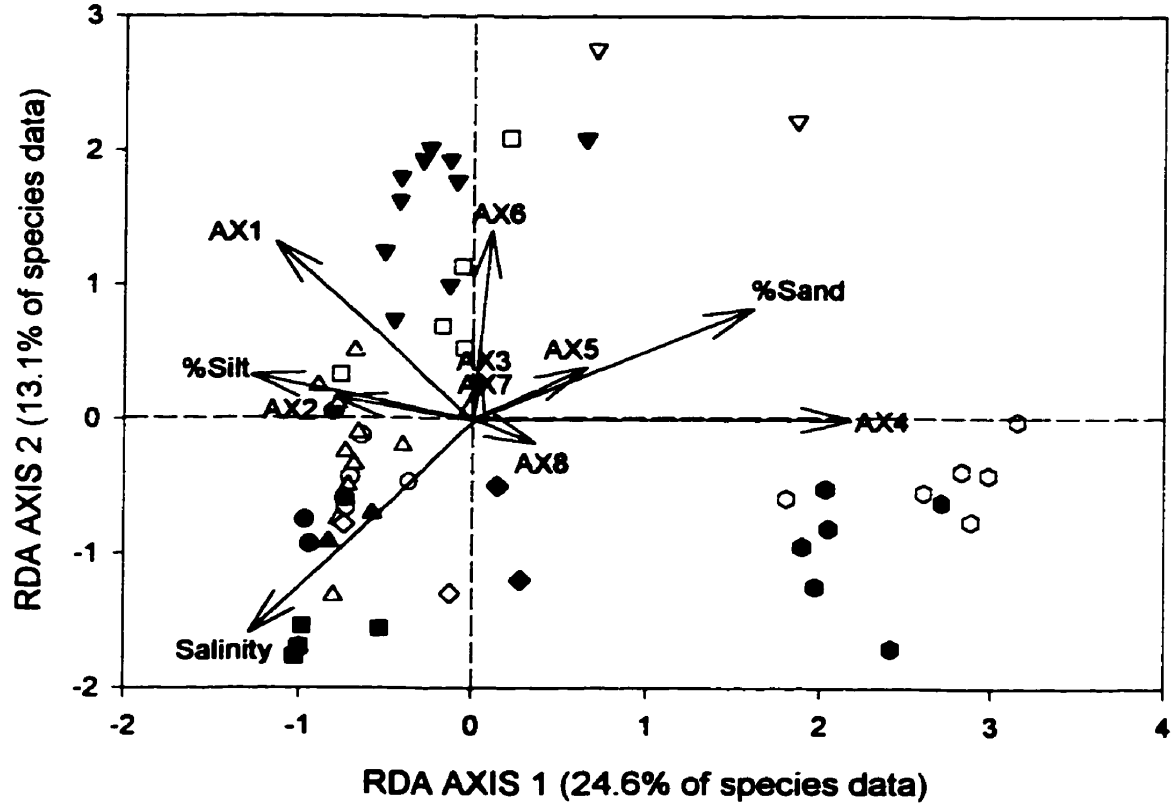
The unique contribution of the modified vegetation variables (26.5%; $p<0.005$) explained more than twice the variability explained by the unique contribution of the soil variables (10.7%; $p<0.005$) (Table 17). This suggests that local seed production

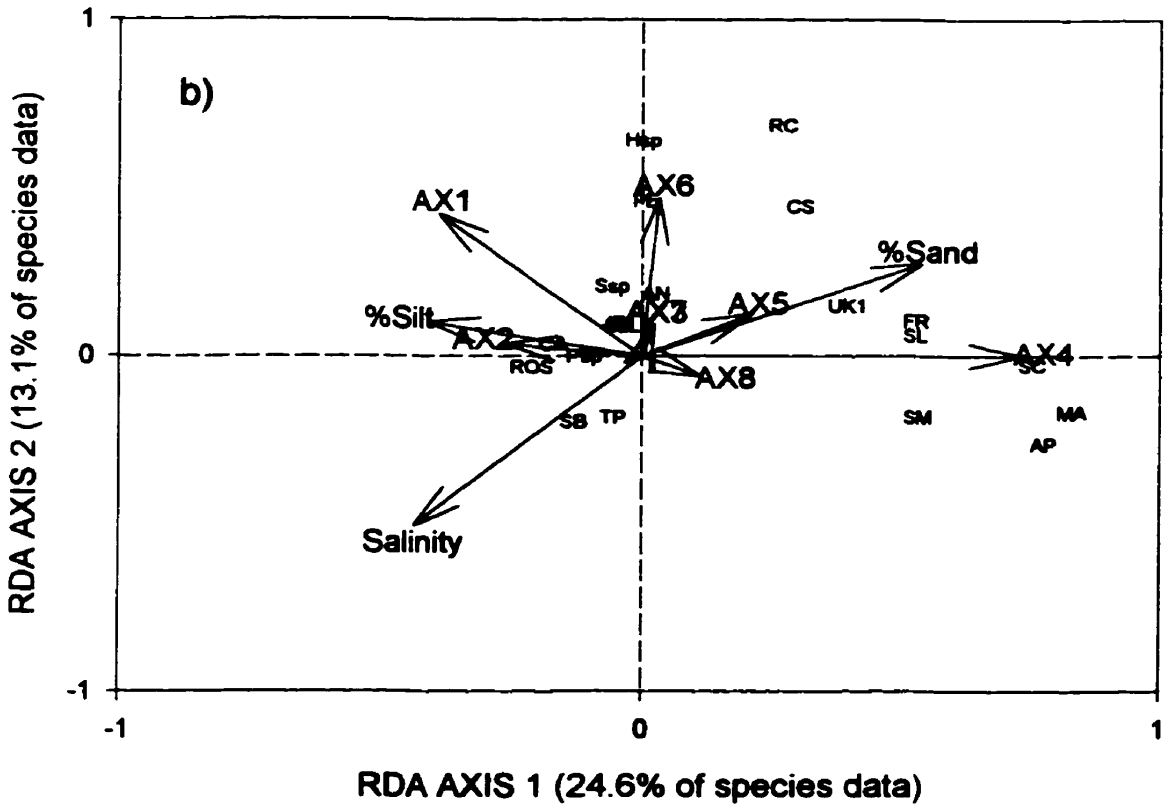
(availability of diaspores) is more important than the two environmental variables *per se* in determining the soil seed bank of an area. However, there is a relatively large interaction factor (15.3%).

Table 18. Species loadings of the vegetation PCA. These first eight axes were used as constraining variables in the seed bank RDA (Fig. 16). The species abbreviations are symbols used in species-variable biplots.

Species Name (including abbreviations)		AX1	AX2	AX3	AX4	AX5	AX6	AX7	AX8
Achillea nigrescens	AN	.1186	.3472	-.0609	.0963	-.1116	.2232	-.1633	.2433
Atriplex patula	AP	.5182	.1189	-.0841	**-.3317**	.3521	-.1407	-.1959	.0349
Calamagrostis deschampsioides	CD	.3750	.6398	.0876	.3350	-.0018	-.1765	.4561	.1692
Carex subspathacea	CS	-.7745	.5235	.2857	-.0045	.0571	-.1409	-.0191	.0278
Dupontia fischeri	DF	-.1472	.2079	.0161	-.1997	.0101	**-.2883**	.0728	.0045
Euphrasia arctica	EA	-.0624	.2945	-.0510	-.0269	-.0838	.2436	-.3192	.1326
Festuca rubra	FR	-.5704	.7162	-.0995	**-.2514**	-.0823	.0713	-.0160	-.0590
Hippuris tetraphylla	HT	.0371	-.0339	.3250	.0226	.0825	.1911	-.1485	-.1219
Hordeum jubatum	HJ	.3229	.1889	-.0795	-.0518	-.0537	.0562	-.0811	-.2388
Koenigia islandica	KI	.1667	-.0382	-.0241	**-.2985**	.2498	-.1065	-.1658	.0110
Juncus bufonius	JB	-.1307	.0542	.3052	.0294	.0706	-.0414	-.1331	.1657
Leymus mollis	LM	.6831	.4157	-.0010	.2866	-.4882	-.0709	-.1452	.0352
Lomatagonium rotatum	LR	.2505	.4780	-.0646	.1125	-.0832	.1028	-.2393	.3275
Matricaria ambigua	MA	.8207	.3382	-.1815	-.2143	.2982	-.1641	-.0587	.0745
Minuartia rubella	MR	.4695	.1854	-.1666	-.1395	.3929	-.1548	.0433	.2644
Parnassia palustris	PaP	-.2243	.1345	.0103	.0482	.0282	-.0976	-.1208	.1080
Plantago maritima	PM	-.3246	-.0145	-.3092	.0407	-.0523	-.0281	-.5184	.3928
Potentilla egedii	PE	-.7021	.6191	-.2397	-.0643	-.0207	.1113	-.0517	.0266
Potentilla norvegica	PoN	.6184	.3536	-.0888	.0958	-.2965	-.0365	-.1171	-.1627
Puccinellia nuttaliana	PN	-.2909	.5150	-.2658	.0201	.1356	**.5387**	.0892	-.1086
Puccinellia phryganodes	PP	-.6596	-.1856	-.4914	**.4968**	.1495	-.0886	-.0211	.0318
Ranunculus cymbalaria	RC	.5331	.5498	-.0829	.2001	.3895	.2766	-.1303	-.1131
Rhinanthus minor	RB	.2564	.1766	-.0647	.0425	-.2139	.0474	-.1188	-.2448
Rumex occidentalis	RO	.2496	.2980	-.0335	-.0009	-.1515	-.0877	-.1386	-.0111
Salicornia borealis	SB	-.0439	-.1802	-.0282	**-.2434**	-.2379	**.5355**	.2016	.5879
Salix brachycarpa	SaB	.0199	.1047	.1080	.2457	.2705	-.2250	.3313	.3092
Salix candida	SaC	-.0713	-.0566	-.1782	.1938	.1283	.2682	-.1714	.0538
Salix planifolia	SaP	-.1950	.2173	-.0976	-.0810	.0527	.3217	-.2726	.2114
Salix spp.	Ssp	.1557	.5651	.0057	.0200	-.4443	**-.2840**	-.1117	.0437
Senecio congestus	SC	.4067	.1868	.6242	**.4477**	.2616	.1959	-.1976	.0386
Senecio pauperculus	SP	.4057	.2541	-.0399	.1439	-.0789	-.0709	.0644	.1733
Spergularia marina	SM	.0536	-.0624	-.0918	-.0290	-.1942	.2697	-.0055	.5477
Stellaria humifusa	SH	-.2241	.4557	-.3126	-.0179	.1951	**.5183**	.0327	-.1819
Stellaria longipes	SL	.6499	.6463	-.2131	.1563	-.0102	.1176	.1346	-.1191
Triglochin palustris	TP	-.0632	-.0159	.6491	**.4344**	.3450	.1380	.0057	.0292
Unknown species 1	UK1	.1951	.2903	-.1180	-.0897	.3768	.1236	-.0183	.3847

Figure 16. Redundancy analysis (RDA) based upon density of species in the soil seed bank constrained by percentage cover of species in the vegetation and three soil variables. Seed bank data were transformed using $y = \log(x + 1)$. AX1 to AX8 are axes resulting from principal component analysis (PCA) of the vegetation data. (a) sample-variable biplot; arrows representing the constraining variables were magnified three times; consult the inset legend in Fig. 14 for explanation of symbols representing samples. (b) species ordination; note difference in scaling from (a), as constraining variable arrows were not magnified. A key to the species abbreviations is given in Table 18.


RDA AXIS 2 (13.1% of species data)
RDA AXIS 1 (24.6% of species data)
AX1
AX6
%Sand
%Silt
AX3
AX5
AX7
AX2
AX4
AX8
Salinity


b)
RDA AXIS 2 (13.1% of species data)
RDA AXIS 1 (24.6% of species data)
RC
Hipp
AX6
AX1
CS
%Sand
Ssp
AX3
AX5
UK1
%Silt
AX2
ROS
AX8
AX4
SB
TP
SM
MA
AP
Salinity

3.4 Discussion

The combination of disturbance and physical stress on plants has had a major effect on the vegetation as predicted overall by Grime (1979). The RDA vegetation ordination (Fig. 14) clearly delineated undamaged areas from where the soil was degraded. As expected, salinity as a stress factor was positively correlated with disturbance and disturbed salt-marsh plots were appreciably more saline than beach-ridge plots. The third axis identified a group of undamaged eastern intertidal plots and one inland exclosure (Fig. 15) on the threshold between undamaged plots and plots where there was loss of vegetation and soil degradation. These former sites are remnants in large areas where surrounding soils are degraded and the encroaching degradation and poor entrapping and establishment conditions may limit regeneration of dicotyledonous species. Most loss of vegetation in the eastern intertidal salt marsh occurred between 1984 and 1986 (Jefferies, unpublished data).

Loss of vegetation has a negative effect on the soil seed bank. While the density of the seed bank was not significantly different between plots with vegetation loss and soil degradation in the western intertidal marsh, the inland salt marsh and on the beach ridge, seed bank density decreased over larger spatial and temporal scales of degradation. This pattern was not always apparent on a smaller scale as the loss of seeds from the soil following vegetation damage is nonlinear and exhibits a threshold property associated with soil erosion. Vegetation loss also leads to the decreasing relative abundance of species characteristic of intact vegetation. In contrast, there is an increase in the relative abundance of invasive species (weedy species or annuals typical of hypersaline mud flats). Due to soil erosion processes, even species with long-term persistent seed banks

are vulnerable to local extinction. The sampled plots in the salt marshes have soil seed banks that reflect different stages in the soil degradation and erosion processes. Plots in the western intertidal marsh, where soil degradation has occurred, have low values for vegetation cover but still retained a relatively rich seed bank. Even though most soil degradation occurred in the western intertidal marsh and in the supratidal marsh at about the same time (1988-1990), soil degradation processes appear to have been slower in the western intertidal salt marsh, possibly because there is less organic matter in those soils which is easily eroded. In the supratidal salt marsh, there were site differences in the seed bank in plots where the vegetation was undamaged indicating spatial heterogeneity in the distribution of the seed bank, which is common (Thompson 1986). These site differences were not apparent in the degraded areas in this marsh.

The inland exclosures also have undamaged vegetation but very poor seed banks composed mostly of *S. borealis*, an indicator of disturbance. Soil degradation was already apparent in the inland marsh during the late 1970s. Although seed production was estimated to be relatively high in at least one of the exclosures, the encroaching soil degradation and rapid run-off of melt water may strongly affect the accumulation of buried seeds. *S. borealis*, present at low frequencies in the exclosed vegetation but the dominant species in the surrounding degraded soils, may have accumulated in high numbers in the soils under the exclosed vegetation due to the easy dispersal of its seeds by water and the presence of outer bracts that act as flotation devices.

Changes in the soil degradation process have been less closely monitored in plots on the beach ridge but most of the change is estimated to have occurred between 1984 and 1985 based on remote-sensing imagery (Jano *et al.* 1998). The effect of loss of

vegetation on the seed banks of the beach ridge was less severe possibly due to the greater number of ruderal species that produce large amounts of seeds in the original vegetation and different degradation processes compared with those of the salt marshes where hypersaline conditions can develop in degraded soils (Srivastava & Jefferies 1996).

The effect of loss of vegetation on the soil seed bank is influenced by the regeneration strategies of plants (Grubb 1977). For example, loss of vegetation and soil degradation were more detrimental to the composition and size of the seed bank in the salt-marsh plots dominated by long-lived perennials than in the beach ridge-plots which have a greater proportion of ruderal species present. Another way of formulating this same statement is that different intensities and types of stress and disturbance select for different regeneration strategies of plants. When disturbance intensity is low, dicotyledonous species increase in abundance in the intertidal salt marsh as shown by their relative abundance in exclosures (Bazely & Jefferies 1986). Many of these plants spread via vegetative means but some contribute to the soil seed bank and when grazing pressure is low, the seed banks can potentially increase in size and in species represented due to greater seed production.

As geese grub for roots and rhizomes, patches in the vegetation appear and are invaded by weedy species that invest heavily in reproduction from seed sources. Soil seed bank density increases but is composed mostly of these invasive species. These patches become increasingly saline as patch size increases (Srivastava & Jefferies 1995a) and eventually, only halophytic annuals such as *S. borealis* can tolerate the high salinity. The seed bank of *S. borealis*, a species at the northern limit of its distribution, is depleted

annually at this location. Fall sampling before the year's seed crop ripened yielded no seed bank.

The degree of similarity between the species composition of vegetation and the soil seed bank is predicted to increase with disturbance due to greater relative abundance of annuals in the vegetation (Hutchings & Russell 1989, Chambers 1993, Ungar & Woodell 1996) and to decrease with "stress" due to lower seed production and greater investment in clonal growth in perennial species (Diemer & Prock 1993). The degree of similarity between the vegetation and the soil seed bank was less in plots where the vegetation was undamaged than in plots where soil was degraded, as shown by similarities and differences in the relative positions in the RDA vegetation and seed bank ordinations (Fig. 14 & Fig. 16). Much of this was due to the fact that the dominant species in undamaged vegetation (*P. phryganodes*, *C. subspathacea*, *L. mollis*) do not contribute at all or very little to the seed bank (also seen in Ungar & Woodell 1996). Dicotyledonous species decline and the monocotyledonous species increase their dominance of the vegetation as grazing pressure increases. *P. phryganodes* is a sterile triploid that has never been known to set viable seed in North America (Bowden 1961, Sadul 1987) and *C. subspathacea* rarely sets seed outside of exclosures due to sustained grazing pressure by geese. In addition to regeneration through rhizomes and stolons, both species can spread through leaf fragments (Chou *et al.* 1992).

Some species were over-represented in the soil seed bank compared to their abundance in the vegetation. Soil seed banks that were dominated by a few species have been shown in other studies including a polar desert in the High Arctic (Freedman *et al.* 1982), a salt marsh near Churchill (Staniforth *et al.* 1998), a high subalpine site in the

Oregon Cascade Mountains (Ingersoll & Wilson 1993), a salt marsh in California (Hopkins & Parker 1984, Staniforth *et al.* 1998), a shoreline in Nova Scotia (Wisheu & Keddy 1991) and dune vegetation in South Africa (Pierce & Cowling 1991). Some species were found in the seed bank but were absent in the present-day vegetation, possibly due to lack of suitable safe sites for germination and establishment (van der Valk & Davis 1976, 1978, 1979, Keddy & Reznicek 1982, Smith & Kadlec 1983). In spite of the low similarity between the vegetation and seed soil seed bank at some plots, roughly half of the seed bank data could be predicted from the vegetation data and vice-versa. These values are slightly inflated as the sample to variable ratio (six to one) is below the ideal (ten to one) (T.J. Carleton, University of Toronto, personal communication).

In conclusion, revegetation potential from the soil seed bank for dicotyledonous species was greater in more recently damaged salt-marsh plots as well as greater in the beach-ridge plots and in salt-marsh plots where the soil degradation was of long standing. However, since the dominant graminoids do not form seed banks, revegetation of the graminoid "template" will be dependent on dispersal of propagules and therefore on the presence of vegetation within dispersal distance. The effect of the vegetation loss on the seed bank was heavily shaped by the life-history strategies of the plants in the original vegetation and site-specific factors also influenced the time lag between loss of vegetation and the subsequent loss of the seed bank in the salt marsh.

Chapter Four: Effect of degradation on seed rain, seed germination and early seedling establishment in the supratidal salt marsh

4.1 Introduction

Gradients of habitat disturbance and of increased stress on plants (*sensu* Grime 1977) are positively correlated at La Pérouse Bay, Manitoba. Grubbing and grazing by increasing numbers of lesser snow geese (*Anser caerulescens caerulescens*) have led to vegetation loss and associated changes in soil abiotic conditions at a landscape level (Jano *et al.* 1998). In the extensive intertidal and supratidal salt marshes that occur in this area, soil degradation is characterized by loss of organic matter, hypersalinity and increased erosion of surface sediments (Srivastava & Jefferies 1996). Grime's model of plant regeneration strategies in relation to gradients of disturbance and stress predicts that no viable strategies exist in habitats subjected to both high disturbance and high stress, and consequently it is predicted that few plants survive in such habitats. The soil seed bank decreases in both density and species richness in response to loss of vegetation, soil degradation and erosion (Chapter Three).

The processes that result in the loss of the soil seed bank, however, can only be understood by investigating seed bank dynamics in these coastal marshes. An important question regarding patterns of regeneration in plant communities is whether recruitment is limited by seed availability (dispersal) or microsite ("safe site") conditions (Klinkhamer & de Jong 1989, Eriksson & Ehrlén 1992). Crawley (1990) suggested in a review that microsite limitation is predominant in regulating recruitment in plant communities. However, Eriksson & Ehrlén (1992) argue that recognition of combined

limitation (both seed and microsite) may prove to be more meaningful in studies of processes controlling recruitment regulation as investigations have shown both types of limitation occur (microsite limitation: Duggan 1985, Crawley & Nachapong 1985, Peart 1989; seed limitation: Fowler 1986, Shaw & Antonovics 1986, Hughes *et al.* 1988, Hughes & Fahey 1988, Peart 1989). In damaged salt marshes at La Pérouse Bay, the factors that potentially constrain recruitment and therefore regeneration of plant communities remain to be assessed.

Loss of vegetation and consequent soil degradation could potentially limit both seed availability and the availability of sites suitable for germination and establishment ("safe-sites" *sensu* Harper 1977). Seed rain is thought to be dominated by local production as the seed rain of plant species typically decreases with distance from the adult plant, although it may achieve its maximum value at some distance away from the source in the case of highly mobile winds flown seeds (Okubo & Levin 1989). Rates of predation may be higher closer to the adult plant (Janzen 1970, Hubbell 1980) but high densities of seeds clumped together may also result in predator satiation (Augspurger & Kitajima 1992). Secondary seed dispersal by wind or water, in addition to patterns of predation, may exert a strong influence on the final distribution of seeds (Smith & Kadlec 1983, Chambers & MacMahon 1994, Inglis 1999). Objectives of this study relating to seed availability included 1) the assessment of the effect of vegetation loss in the local area on the seed rain, as local extinction of a species precludes local production, 2) the appraisal of the distances that seeds disperse and 3) the identification of potentially important seed-dispersing agents.

Some areas in the intertidal and supratidal marshes at La Pérouse Bay still retain relatively rich seed banks but recruitment of seedlings from this source may be limited by hypersalinity which inhibits germination. Hence, a further objective related to the assessment of microsite availability was 4) to evaluate the effect of high soil salinity on seed germination and on early establishment. Seed entrapment and retention processes can be viewed as an interface between seeds and their habitats. The final objectives included determining 5) whether seed entrapment processes were affected by loss of vegetation and 6) whether soil erosion processes had an effect on the retention of seeds in the soil. The resolutions of these objectives are pertinent not only in understanding the degradation process but also the outcomes are important in assessing revegetation potential on degraded marine sediments at La Pérouse Bay. Information on the fate of seeds is a critical aspect in any successful restoration of disturbed ecosystems (Chambers & MacMahon 1994).

4.2 Materials and Methods

4.2.1 Site description

The supratidal salt marsh on the western coast of La Pérouse Bay, Manitoba that is flooded by salt water very occasionally (two to three times every three years) is dominated by low willow shrubs (*Salix brachycarpa, Salix myrtillifolia*) which develop on frost-heaved hummocks. Two caespitose grasses, *Festuca rubra, Calamagrostis deschampsioides*, grow in association with these shrubs while a graminoid sward consisting of *Puccinellia phryganodes* and *Carex subspathacea* covers lower-lying areas between hummocks where saline sediments are exposed. Associated dicotyledonous

species in this graminoid sward include *Potentilla egedii, Plantago maritima, Ranunculus cymbalaria* and *Stellaria humifusa*. Ruderals such as *Senecio congestus* and *Salicornia borealis* colonize disturbed areas. All of these species exhibit varying levels of salt-tolerance. *S. brachycarpa, S. myrtillifolia, F. rubra* and *C. deschampsioides* are species at one end of the gradient that are sensitive to salt and *S. borealis*, the most tolerant species is at the other end of the salinity gradient. *Puccinellia phryganodes* and *Carex subspathacea* are able to tolerate moderate levels of salinity (Srivastava & Jefferies 1995b)

Willow-grassland is also present along the banks and in the vicinity of the Mast River, northwest of the supratidal marsh. In these locations, the shrub layer is composed of three willow species, *S. planifolia, S. candida* and *S. lanata* together with *Myrica gale* and *Betula glandulosa*. Sedge meadows dominated by *Carex aquatilis* occur in close proximity away from the influence of the highest tides. All of these species are less tolerant of high salinity than those species that grow in the salt marsh. A detailed description of the vegetation is given in Jefferies *et al.* 1979 and Jano *et al.* 1998.

4.2.2 Collection of seed rain data

Seed rain data were collected from two sites showing loss of vegetation and soil degradation and two undamaged sites in the supratidal salt marsh on the west side of La Pérouse Bay, based on seeds collected in seed traps (30cm by 30cm) made of artificial lawn material. The artificial lawn material is made of green, plastic strands woven in a carpet and may be purchased at most hardware stores. Site 1 (undamaged marsh) was the most proximate to the fresh-water system and occurred less than 100 m east of the Mast

River. The other sites were at least 1 km east of Site 1. At each site, seed traps were set up at twelve plots and emptied once every six to ten days during the growing season. We emptied the traps by shaking the artificial lawn material vigorously in plastic bags. The plots were identical to those used to sample the seed bank and vegetation cover abundance except for two additional plots added to each site. Additional plots were added so that a total area of one square metre would be sampled at each site. The seed rain was sampled for two consecutive years in 1997 and 1998 during the growing season. In addition, seed traps were also left intact during the winter of 1997 in order to measure seed inputs during the spring melt in 1998.

4.2.3 Effect of salinity on seed germination

An assay on the effect of salinity on germination was conducted for fifteen species found in the supratidal salt marsh on the west side of La Pérouse Bay. Seeds were sampled haphazardly from plants as close to the time of dispersal as possible during the summer of 1997. They were air-dried and separated from the chaff manually or by using sieves. They were then placed in a freezer (-8.7°C) for four months as chilling has been shown to increase the percentage of seeds that germinate at low constant temperatures in woody tundra and taiga species (Gartner 1983). Cold stratification substantially lowered the temperature where seeds would germinate and broke the dormancy in most of the arctic species studied by Densmore (1979) (as reviewed in Gartner 1983). Subsequently, the samples were subjected to three weeks of freeze-thaw cycles (5°C for three days followed by two days at -8°C in the dark) to simulate the field conditions and induce scarification (Gartner 1983). Six species (*Ranunculus cymbalaria, Plantago maritima, , Festuca*

rubra, Hippuris tetraphylla, Senecio congestus and *Leymus mollis*) were tested for germination at different salinities in May 1997 and, due to time constraints, eight species (*Parnassia palustris, Primula* spp., *Castilleja raupi, , Betula glandulosa, Matricaria ambigua, Rhinanthus minor, Hippuris vulgaris* and *Salix brachycarpa*) were maintained for a year at 5°C and tested for germination during May 1998. Seeds of *Potentilla egedii* and *Salicornia borealis* were assayed for germination in both years. For *P. egedii*, the assays were conducted using seeds collected in 1997 for both years. *S. borealis* seeds were collected in both 1997 and 1998,

Four salinity treatments of 0%, 5%, 20% and 60% the strength of oceanic seawater (~34 grams of dissolved solutes per litre) were used in the assay. Salinity solutions were prepared from Instant Ocean salts (Aquarium System, 8141 Tyler Boulevard, Mentor, Ohio 44060, USA). Eight 20-seed replicates of each species were placed in sterilized Petri dishes (diameter of 60 mm, depth of 15 mm) with loose covers on top of silica sand and to which was added 5 ml of the appropriate solution. The Petri dishes were placed randomly on counter space next to windows in the laboratory and kept at room temperature (~22°C) and ambient light conditions. High temperatures (20-30°C) and light levels have been shown to enhance germination of many Arctic species (Bliss 1958, Gartner 1983). Additional solution was added as needed and the dishes were monitored daily for a period of 30 days. Germination was defined as the emergence of the radicle. Seeds were removed as soon as germination occurred.

4.2.4 Effect of salinity on early establishment

Intact soil cores with attached vegetation were collected along a soil degradation gradient (high biomass to low biomass as categorized by Srivastava & Jefferies 1995a and bare ground) from the *Puccinellia phryganodes-Carex subspathacea* assemblage and from the *Festuca rubra-Calamagrostis deschampsioides* assemblage in the supratidal salt marsh on 6 June, 1994 in the general vicinity of the sites that were sampled for seed rain. Four sites were sampled beneath each of these vegetation types. Twenty intact soil cores with attached vegetation were taken from the ground at each site. Ten of these cores were placed in flower pots (diameter of 10.5 cm, depth of 10 cm) and placed randomly in a common garden where they were watered twice a day with river water. Ten of these cores were replanted into the ground in flower pots from which they were taken. Therefore, 160 pots, in total, were kept in the common garden and 160 pots were left in the field.

All seedlings of dicotyledonous plants present in these plots were counted every seven to fourteen days from early June until early August, 1994. For *Plantago maritima* and *Potentilla egedii*, seedlings were difficult to distinguish from plant resprouting from underground organs. The last day plants were monitored in the field was 27 July and in the common garden on 1 August, 1994. At the end of the experiment, all above ground biomass was harvested from both pots in the field and in the common garden on 2 August, 1994. The turves were trimmed into 5 cm x 5 cm squares, their above ground biomass was clipped, placed in a tray of water and washed and sorted according to species. The biomass of monocotyledonous species was pooled within each pot. Plant material was then dried using a radiant heat oven (Lab-Line Imperial II, Johns Scientific,

Toronto) and weighed using a balance (Mettler PE 160, Mettler Instrumente, AG CH-8606, Grenifensee, Zürich).

A turf with attached organic soil (10 cm x 10 cm) was collected initially from all 16 sites in order to measure the salinity of the soil water. Thereafter, samples were taken from two randomly chosen sites for each vegetation type (i.e. high/low biomass Puccinellia-Carex assemblages, bare ground and Festuca-Calamagrostis assemblages) every ten to fifteen days. For the common garden, a salinity sample was taken from two randomly picked pots originating from each vegetation type on August 2. Early in the season, soil water was extracted by manually squeezing the samples but as soils became drier, soil samples were centrifuged and the extracted soil water was diluted with de-ionized water (Srivastava & Jefferies 1995a). Soil salinity (grams of solute per litre of water) and soil conductivity (reciprocal ohms) were measured using a salinity/ conductivity meter (Yellow Springs, Ohio, Model 33). As soil samples became drier and only small volumes of water could be extracted, the test solution samples were increasingly diluted with deionized water until it was possible to measured only conductivity with the Yellow Springs meter. Conductivity measurements were calculated back to salinity using a simple linear regression between paired values collected for salinity and conductivity.

4.3 Results

4.3.1 Seed rain

The seed rain was low (<3 seeds m^{-2} per day) during the growing season of 1997 (Fig. 17). The highest densities representing the seed input were measured during mid-to-late

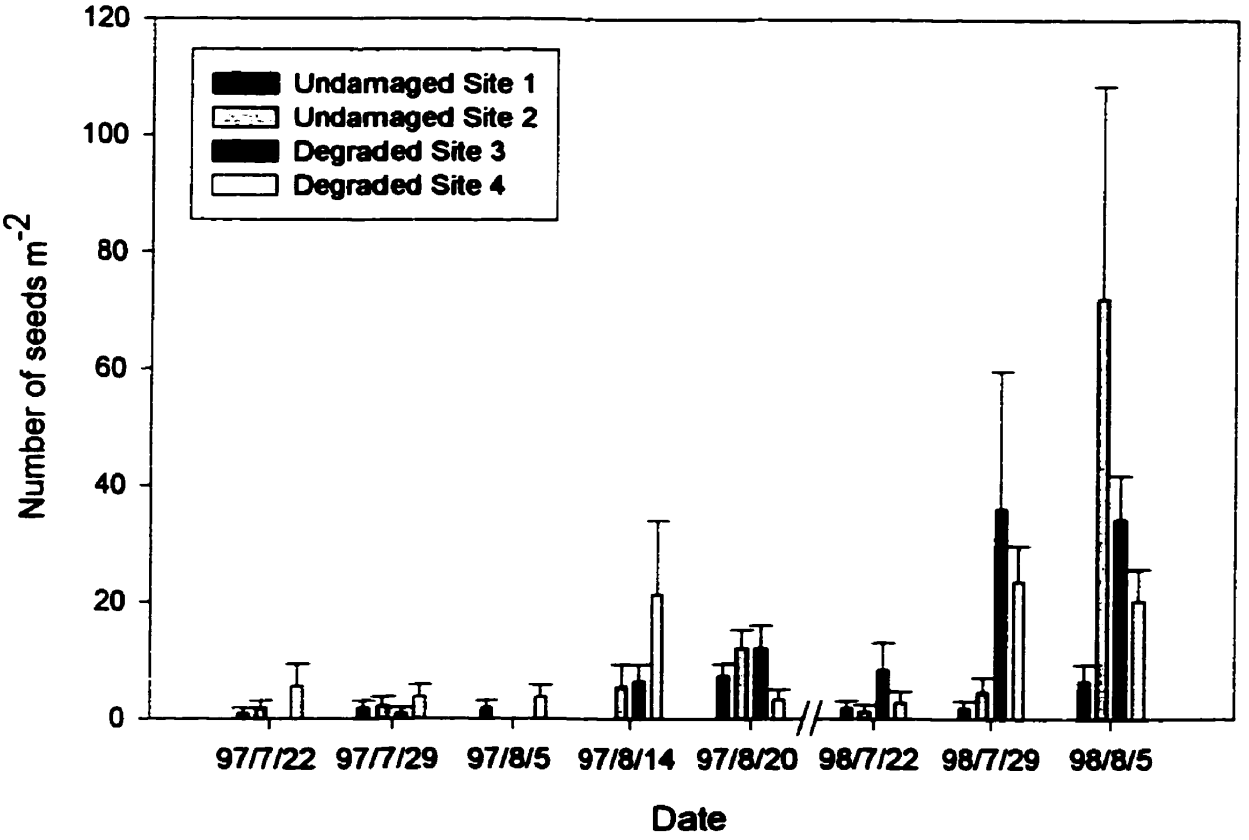


Figure 17. Seed rain (density of seeds m^{-2} ± standard error) collected during two consecutive growing season in 1997 and 1998.

August with seeds of *P. egedii* (29%), *S. congestus* (17%), *Carex* spp. (10%) and *B. glandulosa* (7%) contributing most to the cumulative seed rain (Table 19). There was no significant difference in the total number of seeds caught in undamaged vegetation plots from those caught on degraded soils (Wilcoxon-rank sum test, n=24, m=24, W_n=532, n.s.). During the growing season of 1998, the total numbers of seeds caught from the seed rain was significantly larger than that caught during the previous season (Sign test for paired replicates, n=48, r=5, $p<<0.001$) and most seeds were trapped in late July and early August (Fig. 17). The cumulative seed rain was mostly composed of wind-dispersed seeds of willow shrubs (56%) and fresh-water species, *C. aquatilis* (25%) and *M. gale* (7%) (Table 20). The seed rain sampled from undamaged vegetation plots was significantly lower than the seed rain sampled from degraded soils (Wilcoxon rank-sum test, n=24, m=24, W_n=466.5, $p<0.01$).

The number of seeds caught in the seed traps was significantly greater during the spring melt, when seeds were undergoing secondary dispersal, than during the previous growing season (Sign test for paired replicates, n=40, r=3, $p<0.001$) (Fig. 18). The salt-tolerant ruderal, *S. borealis*, was the main constituent of the seed rain (38%) followed by the fresh-water species, *Myrica gale* (14%), *C. aquatilis* (12%), *B. glandulosa* (10%) and *P. palustris* (10%), and the brackish species, *Hippuris* spp. (7%) (Table 21). The number of seeds caught in the undamaged vegetation was not significantly different from that caught in the bare soils (Wilcoxon rank-sum test, n=19, m=21, W_n=400.5, n.s.).

Table 19. Density of seeds (seeds m^{-2}) trapped in supratidal salt marsh during the 1997 growing season.

Species	97/7/22				97/7/29			
	Undamaged		Degraded		Undamaged		Degraded	
	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=12)	Site 4 (N=12)	Site 1 (N=12)	Site 2 (N=10)	Site 3 (N=12)	Site 4 (N=12)
Salt-Marsh Graminoid Sward								
Potentilla egedii	0	0	0	3.7±3.7	0	0	0	0.92±0.92
Ranunculus cymbalaria	0	0	0	0	0	0	0	0
Salt-Marsh Willow-Grassland								
Calamagrostis spp.	0	0	0	0	0	0	0	0
Lomatogonium rotatum	0	0	0	0	1.8±1.2	0	0	0
Salix spp.	0	0	0	0	0	1.1±1.1	0	0
Hypersaline Mudflats								
Salicornia borealis	0	0	0	0	0	0	0	1.8±1.8
Atriplex patula	0	0	0	0	0	0	0	0
Freshwater Marsh Willow-Grassland								
Betula glandulosa	0	0	0	0	0	1.1±1.1	0.92±0.92	0
Carex gynocrates	0	0	0	0	0	0	0	0
Myrica gale	0	0	0	0	0	0	0	0
Saxifraga hirculis	0	0	0	0	0	0	0	0
Brackish Ponds & Streams								
Hippuris spp.	0	0.92±0.92	0	0	0	0	0	0
Freshwater Ponds & Streams								
Carex aquatilis	0	0.92±0.92	0	0	0	0	0	0
Potamogeton filiformis	0	0	0	0	0	0	0	0
Potentilla palustris	0	0	0	0	0	0	0	0
Weedy								
Juncus bufonius	0	0	0	0	0	0	0	0
Matricaria ambigua	0	0	0	0.92±0.92	0	0	0	0
Senecio congestus	0.92±0.92	0	0	0	0	0	0	0
Other								
Carex spp.	0	0	0	0	0	0	0	0
Gramineae	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0.92±0.92	0	0	0	0.92±0.92
Total	0.92±0.92	1.85±1.25	0	5.6±3.7	1.8±1.2	2.2±1.5	0.92±0.92	3.7±2.1

Table 19. (cont.) Density of seeds (seeds m^{-2}) trapped in supratidal salt-marsh during the 1997 growing season.

Species	97/8/5				97/8/14			
	Undamaged		Degraded		Undamaged		Degraded	
	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=11)	Site 4 (N=12)	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=12)	Site 4 (N=12)
Salt-Marsh Graminoid Sward								
Potentilla egedii	0	0	0	0	0	0	1.8±1.2	17±13
Ranunculus cymbalaria	0	0	0	0	0	0	0	0
Salt-Marsh Willow-Grassland								
Calamagrostis spp.	0	0	0	0	0	0	0	0
Lomatogonium rotatum	0	0	0	0	0	0	0	0
Salix spp.	0	0	0	0	0	0	0	0
Hypersaline Mudflats								
Salicornia borealis	0	0	0	0	0	0	0	0
Atriplex patula	0	0	0	0	0	0	0	0
Freshwater Marsh Willow-Grassland								
Betula glandulosa	0	0	0	0	0	0	0	0
Carex gynocrates	0	0	0	0	0	0	0	0.92±0.92
Myrica gale	0	0	0	0	0	0	0	0
Saxifraga hirculis	0	0	0	0	0	0	0	0
Brackish Ponds & Streams								
Hippuris spp.	0	0	0	0	0	0	0	0
Freshwater Ponds & Streams								
Carex aquatilis	0	0	0	0	0	3.7±3.7	0.92±0.92	0.92±0.92
Potamogeton filiformis	0	0	0	0	0	0.92±0.92	0	0
Potentilla palustris	0	0	0	0	0	0.92±0.92	0	0
Weedy								
Juncus bufonius	0	0	0	0	0	0	0.92±0.92	0
Matricaria ambigua	0	0	0	0	0	0	0	0
Senecio congestus	1.8±1.2	0	0	3.7±2.1	0	0	0.92±0.92	0
Other								
Carex spp.	0	0	0	0	0	0	0.92±0.92	2.8±1.4
Gramineae	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0	0	0	0.92±0.92	0
Total	1.8±1.2	0	0	3.7±2.1	0	5.6±3.7	6.5±2.9	21±13

Table 19. (cont.) Density of seeds (seeds m^{-2}) trapped in supratidal salt-marsh during the 1997 growing season.

Species	97/8/20				Cumulative Total for 1997			
	Undamaged		Degraded		Undamaged		Degraded	
	Site 1 (N=12)	Site 2 (N=10)	Site 3 (N=12)	Site 4 (N=10)	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=12)	Site 4 (N=12)
Salt-Marsh Graminoid Sward								
Potentilla egedii	0.92±0.92	0	0.92±0.92	1.1±1.1	0.92±0.92	0	2.8±1.4	22±14
Ranunculus cymbalaria	0	0	0	0	0	0	0	0
Salt-Marsh Willow-Grassland								
Calamagrostis spp.	0	0	0	0	0	0	0	0
Lomatogonium rotatum	0	0	0	0	1.8±1.2	0	0	0
Salix spp.	0	1.1±1.1	0	0	0	1.8±1.2	0	0
Hypersaline Mudflats								
Salicornia borealis	0	0	0.92±0.92	0	0	0	0.92±0.92	1.8±1.8
Atriplex patula	0	0	0	0	0	0	0	0
Freshwater Marsh Willow-Grassland								
Betula glandulosa	0	5.6±7.8	0	0	0	5.6±2.2	0.92±0.91	0
Carex gynocrates	0	2.2±1.5	0	0	0	1.8±1.2	0	0.92±0.92
Myrica gale	0	1.1±1.1	0	0	0	0.92±0.92	0	0
Saxifraga hirculis	0	0	0	0	0	0	0	0
Brackish Ponds & Streams								
Hippuris spp.	0	0	3.7±3.7	0	0	0.92±0.92	3.7±3.7	0
Freshwater Ponds & Streams								
Carex aquatilis	0	0	0.92±0.92	0	0	4.6±3.7	1.8±1.2	0.92±0.92
Potamogeton filiformis	0	0	0	1.1±1.1	0	0.92±0.92	0	0.92±0.92
Potentilla palustris	0	0	0.92±0.92	0	0	0.92±0.92	0.92±1.92	0
Weedy								
Juncus bufonius	0	0	0	0	0	0	0.92±0.92	0
Matricaria ambigua	0	0	0	0	0	0	0	0.92±0.92
Senecio congestus	5.6±1.7	1.1±1.1	0.92±0.92	0	8.3±2.0	0.92±0.92	1.8±1.2	3.7±2.1
Other								
Carex spp.	0.92±0.92	1.1±1.1	3.7±2.1	0	0.92±0.92	0.92±0.92	4.6±2.5	2.8±1.4
Gramineae	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	1.1±1.1	0	0	0.92±0.92	2.8±1.4
Total	7.4±2.1	12±3.1	12±4.0	3.3±1.7	12.0±2.5	19.4±5.5	19.4±5.0	37±13

Table 20. Density of seeds (seeds m-2) trapped in supratidal salt-marsh during the 1998 growing season.

Species	98/7/22				98/7/29			
	Undamaged		Degraded		Undamaged		Degraded	
	Site 1 (N=12)	Site 2 (N=9)	Site 3 (N=12)	Site 4 (N=12)	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=8)	Site 4 (N=8)
Salt-Marsh Graminoid Sward								
Potentilla egedii	0	0	0	0	0	0	0	1.4±1.4
Ranunculus cymbalaria	0	0	0	0	0	0	0	0
Salt-Marsh Willow-Grassland								
Calamagrostis spp.	0	0	0	0	0	0	0	0
Lomatogonium rotatum	0	0	0	0	0	0	0	0
Salix spp.	0.92±0.92	1.2±1.2	0.92±0.92	0	0	2.8±2.0	9.7±4.4	4.2±2.9
Hypersaline Mudflats								
Salicornia borealis	0	0	0.92±0.92	1.8±1.8	0	0	0	1.4±1.4
Atriplex patula	0	0	0	0	0	0	0	0
Freshwater Marsh Willow-Grassland								
Betula glandulosa	0	0	0	0	0	0	5.6±5.6	0
Carex gynocrates	0	0	0	0	0	0	0	0
Myrica gale	0	0	0	0.92±0.92	0	0	8.3±8.3	8.3±4.6
Saxifraga hirculis	0	0	0	0	0	0	1.4±1.4	0
Brackish Ponds & Streams								
Hippuris spp.	0.92±0.92	0	0.92±0.92	0	0.92±0.92	0	0	1.4±1.4
Freshwater Ponds & Streams								
Carex aquatilis	0	0	4.6±4.6	0	0	0	11±9.6	5.6±4.2
Potamogeton filiformis	0	0	0	0	0	0	0	0
Potentilla palustris	0	0	0	0	0	0.92±0.92	0	0
Weedy								
Juncus bufonius	0	0	0	0	0	0	0	0
Matricaria ambigua	0	0	0	0	0	0	0	0
Senecio congestus	0	0	0	0	0.92±0.92	0.92±0.92	0	0
Other								
Carex spp.	0	0	0.92±0.92	0	0	0	0	0
Gramineae	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0	0	0	0	1.4±1.4
Total	1.8±1.2	1.2±1.2	8.3±4.8	2.8±2.0	1.8±1.2	4.6±2.5	36±24	24±6.1

Table 20. (cont.) Density of seeds (seeds m^{-2}) trapped in supratidal salt-marsh during the 1998 growing season.

Species	98/8/5				Cumulative Total for 1998			
	Undamaged		Degraded		Undamaged		Degraded	
	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=11)	Site 4 (N=12)	Site 1 (N=12)	Site 2 (N=12)	Site 3 (N=12)	Site 4 (N=12)
Salt-Marsh Graminoid Sward								
Potentilla egedii	0	0	0	0	0	0	0	0.92±0.92
Ranunculus cymbalaria	0	0	0	0	0	0	0	0
Salt-Marsh Willow-Grassland								
Calamagrostis spp.	0	0	0	0	0	0	0	0
Lomatogonium rotatum	0	0	0	0	0	0	0	0
Salix spp.	5.6±2.9	40±24	32±7.2	18±5.9	6.5±3.2	44±24	37±9.9	20±6.8
Hypersaline Mudflats								
Salicornia borealis	0	0	0	0	0	0	0.92±0.92	2.8±2.0
Atriplex patula	0	0	0	0	0	0	0	0
Freshwater Marsh Willow-Grassland								
Betula glandulosa	0	0.92±0.92	1.0±1.0	0	0	0.92±0.92	4.6±2.7	0
Carex gynocrates	0	0	0	0	0	0	0	0
Myrica gale	0	0	0	0.92±0.92	0	0	5.6±5.6	7.4±3.7
Saxifraga hirculis	0	0	1.0±1.0	0	0	0	1.8±1.2	0
Brackish Ponds & Streams								
Hippuris spp.	0	0	0	0	1.8±1.2	0	0.92±0.92	0.92±0.92
Freshwater Ponds & Streams								
Carex aquatilis	0	31±31	0	1.8±1.8	0	31±31	12±7.5	5.6±3.2
Potamogeton filiformis	0	0	0	0	0	0	0	0
Potentilla palustris	0.92±0.92	0	0	0	0.92±0.92	0.92±0.92	0	0
Weedy								
Juncus bufonius	0	0	0	0	0	0	0	0
Matricaria ambigua	0	0	0	0	0	0	0	0
Senecio congestus	0	0	0	0	0.92±0.92	0.92±0.92	0	0
Other								
Carex spp.	0	0	0	0	0	0	0.92±0.92	0
Gramineae	0	0	0	0	0	0	0	0
Umbelliferae	0	0	0	0	0	0	0	0.92±0.92
Total	6.5±2.9	72±36	34±7.6	20±5.4	10.2±3.2	78±36	64±20.1	39±6.3

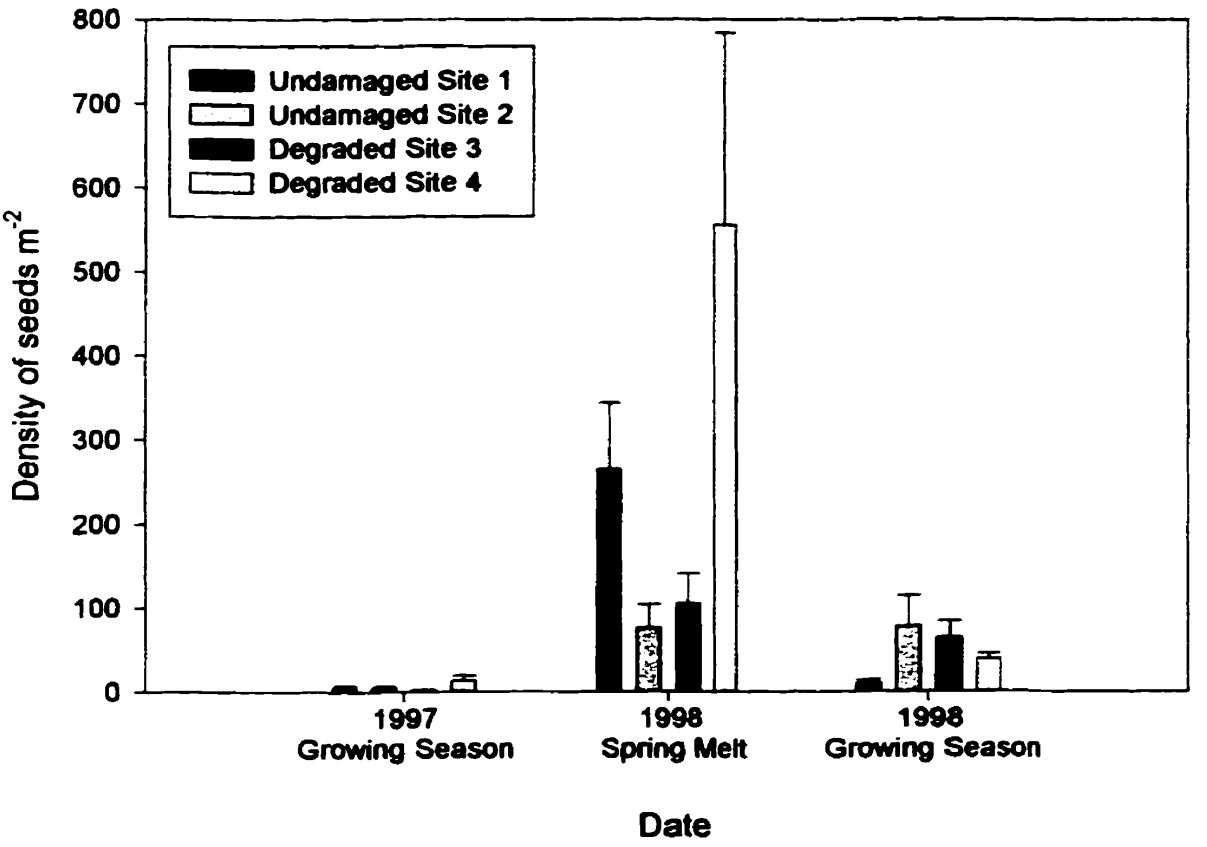


Figure 18. Cumulative seed rain (density of seeds m^{-2} ± standard error) on three sampling dates (July 22, July 29 and August 5) for growing seasons of 1997 and 1998 and for the spring melt in 1998. Two sites were sampled in both the undamaged supratidal salt marsh and supratidal salt marsh where loss of vegetation and soil degradation had occurred (N=12 for each site sampled during the 1997 and 1998 growing season; for spring-melt data, N=12 for Site 1, N=10 for Site 2, N=11 for Site 3, N=8 for Site 4). Consult inset legend for coding of sites and conditions.

Table 21. Density of seeds (seeds m^{-2}) trapped in supratidal salt-marsh during the 1998 spring melt.

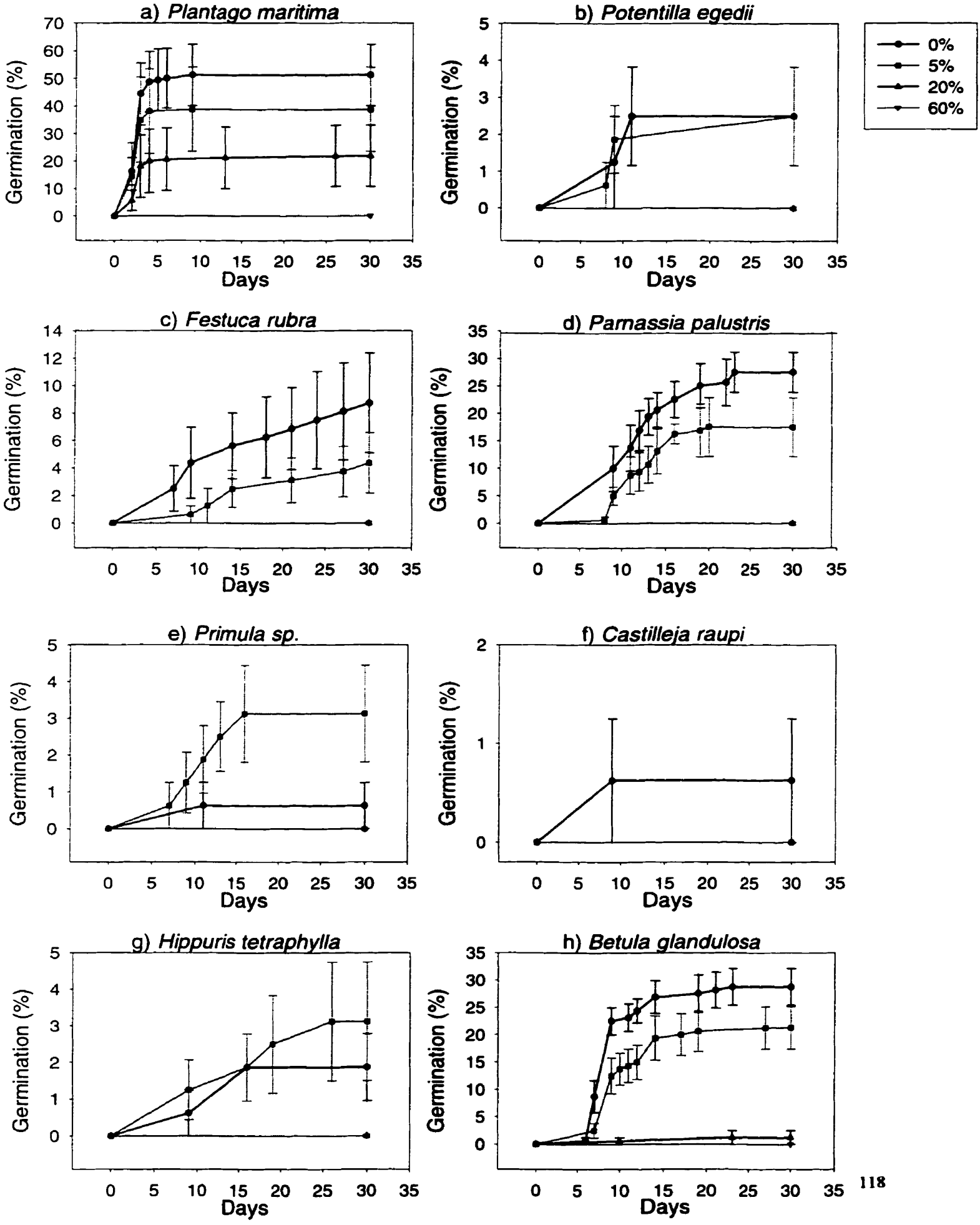
Species	98/6/7			
	Undamaged		Degraded	
	Site 1 (N=11)	Site 2 (N=10)	Site 3 (N=11)	Site 4 (N=8)
Salt-Marsh Graminoid Sward				
Potentilla egedii	21±9.7	1.1±1.1	1.0±1.0	2.8±1.8
Ranunculus cymbalaria	2.0±1.4	0	0	0
Salt-Marsh Willow-Grassland				
Calamagrostis spp.	0	0	0	6.9±6.9
Lomatogonium rotatum	0	0	0	0
Salix spp.	0	0	0	0
Hypersaline Mudflats				
Salicornia borealis	87±57	4.4±3.0	25±18	260±150
Atriplex patula	3.0±2.2	0	0	0
Freshwater Marsh Willow-Grassland				
Betula glandulosa	14±12	21±6.7	9.1±4.2	56±25
Carex gynocrates	0	2.2±1.5	0	1.4±1.4
Myrica gale	52±25	19±9.2	35±30	32±15
Saxifraga hirculis	0	1.1±1.1	0	0
Brackish Ponds & Streams				
Hippuris spp.	44±21	4.4±2.4	7.1±5.0	14±11
Freshwater Ponds & Streams				
Carex aquatilis	16±14	3.3±1.7	11±3.0	89±38
Potamogeton filiformis	2.0±1.4	0	2.0±1.4	0
Potentilla palustris	12±5.5	19±12	8.1±3.4	61±39
Weedy				
Juncus bufonius	7.1±4.0	0	0	0
Matricaria ambigua	0	0	0	0
Senecio congestus	1.0±1.0	0	0	2.8±2.8
Other				
Carex spp.	0	0	0	0
Gramineae	1.0±1.0	0	3.0±1.6	0
Umbelliferae	2.0±1.4	0	2.0±1.4	29±24
Total	260±78	76±82	100±27	560±43

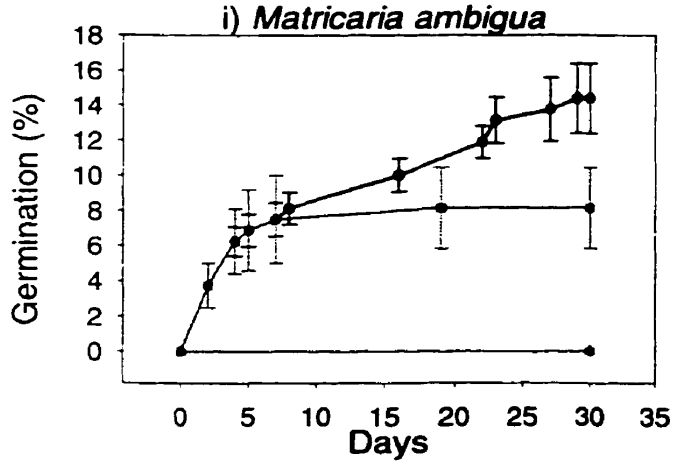
4.3.2 Germination and salinity

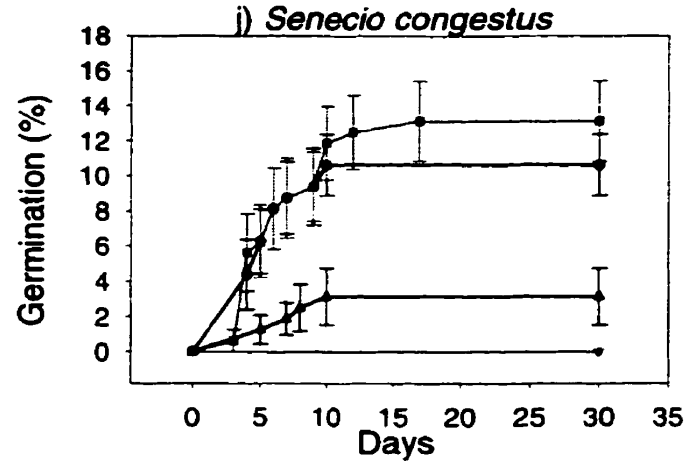
The overall cumulative germination was highest for seeds of *P. maritima* (up to 50%), *P. palustris* (up to 27%) and *Betula glandulosa* (up to 27%) (Fig. 19). Very few seeds germinated (<5%) in four of the tested species, *Primula* spp., *Hippuris tetraphylla*, *Castilleja raupi* and *Potentilla egedii*. Increasing salinity had a detrimental effect on the seed germination of all species. The greatest percentage of seeds germinated in distilled water and declined progressively in solutions salinities of 5%, 20% and 60% the strength of oceanic seawater. Seeds of the halophyte, *P. maritima*, had a relatively high rate of germination (20%) in the 20% sea water solution compared to other species. The only other species able to germinate at even low percentages (<5%) in the 20% sea water solution were *S. congestus*, *L. mollis* and *B. glandulosa*. No species was able to germinate in the solution which was 60% the strength of sea water solution.

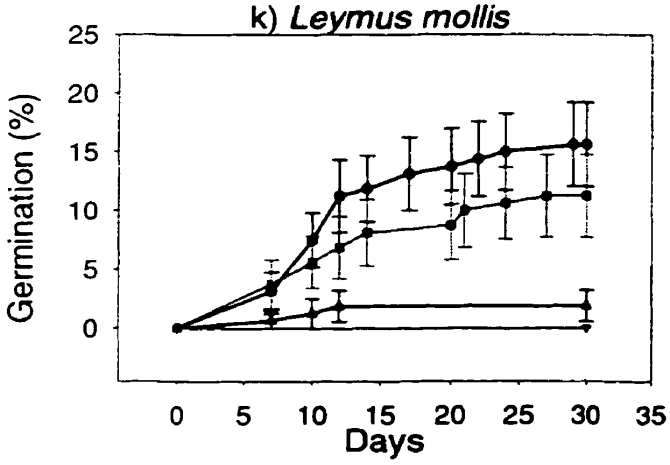
Seeds of five species, *Ranunculus cymbalaria*, *H. vulgaris*, *S. brachycarpa*, *S. borealis* and *Rhinanthus minor*, did not germinate at all. All of these species, except *R. cymbalaria*, suffered from high levels of fungal attack. A fungicide was not used as Baskin & Baskin (1998) suggests that inferior seeds would be more likely be attacked by fungi. A small percentage of *P. egedii* seeds germinated during 1998 but did not germinate at all during the 1997. In three of the species, *H. tetraphylla*, *H. vulgaris*, *P. maritima* and *P. egedii*, the seed coat became mucilaginous upon wetting. In such states the adverse osmotic and ion effects of high salinity may be reduced by the presence of gel-like materials (Ungar 1991).

Figure 19. Cumulative percentage of seeds (± standard error) that germinated in solutions that were 0%, 5%, 20% and 60% the salinity of oceanic seawater. Eight 20-seed replicates were used in the germination assay. Note different scales. Logistic regression on the cumulative germination percentage indicated that germination of *Matricaria ambigua* (df=1, X^2=11.20, p<001), *Betula glandulosa* (df=1, X^2=9.78, p<0.005), *Parnassia palustris* (df=1, X^2=9.33, p<005), *Plantago maritima* (df=1, X^2=6.35, p=0.01), *Leymus mollis* (df=1, X^2=7.27, p<0.01), *Festuca rubra* (df=1, X^2=5.19, p<0.05) and *Senecio congestus* (df=1, X^2=4.07, p<0.05) was significantly related to salinity treatment.


a) Plantago maritima
b) Potentilla egedii
c) Festuca rubra
d) Parnassia palustris
e) Primula sp.
f) Castilleja raupi
g) Hippuris tetraphylla
h) Betula glandulosa
Germination (%)
Days
0%
5%
20%
60%


i) Matricaria ambigua
Germination (%)
0
2
4
6
8
10
12
14
16
18
0 5 10 15 20 25 30 35
Days


j) Senecio congestus
Germination (%)
0
2
4
6
8
10
12
14
16
18
0 5 10 15 20 25 30 35
Days


k) Leymus mollis
Germination (%)
0
5
10
15
20
25
0 5 10 15 20 25 30 35
Days

4.3.3 Salinity and early seedling establishment

The salinity of soil water samples taken later in the season, as the soils became drier, was estimated from the conductivity using a regression equation (Fig. 20). The regression was highly significant ($p<0.001$) and explained a very high proportion of the variability (98.6%). In the control plots, salinity increased as the season progressed (from 1-10 g of solute per litre to 25-60 g of solute per litre) and salinity was higher in soils where there was either bare ground or low biomass of *Puccinellia-Carex* compared with soils with a high biomass of *Puccinellia-Carex* and *Festuca-Calamagrostis* (Fig. 21). Watering the pots decreased the salinity of interstitial water at least one order of magnitude.

Lowering the salinity by watering with river water significantly increased the standing crop of graminoids in the pots (square root transformation, two-sample *t* test, $df = 1$, $t = 10.265$, $p<<0.001$) (Fig. 22a). Pots that originated from swards of *Puccinellia-Carex* with a high biomass had the highest standing crop followed by low biomass swards of *Puccinellia-Carex* and *Festuca-Calamagrostis*. Pots taken from bare ground sites had the lowest standing crop of all samples (Tukey-Kramer multiple comparisons, family error rate = 0.05). Site differences existed only in pots taken from bare ground sites and *Festuca-Calamagrostis* swards (Tukey-Kramer multiple comparisons, family error rate = 0.05).

Both measurements of standing crop and counts of plants found per pot showed that growth and early establishment of *P. egedii* (Fig. 22b, Fig. 23a), *P. maritima* (Fig. 22c, Fig. 23b) and *Salix* spp. (Fig. 22e, Fig. 23d) generally increased with watering. The *Festuca-Calamagrostis* swards had the highest standing crop and number of *P. egedii* plants followed by the high biomass *Puccinellia-Carex* swards. Plants of *P. maritima*

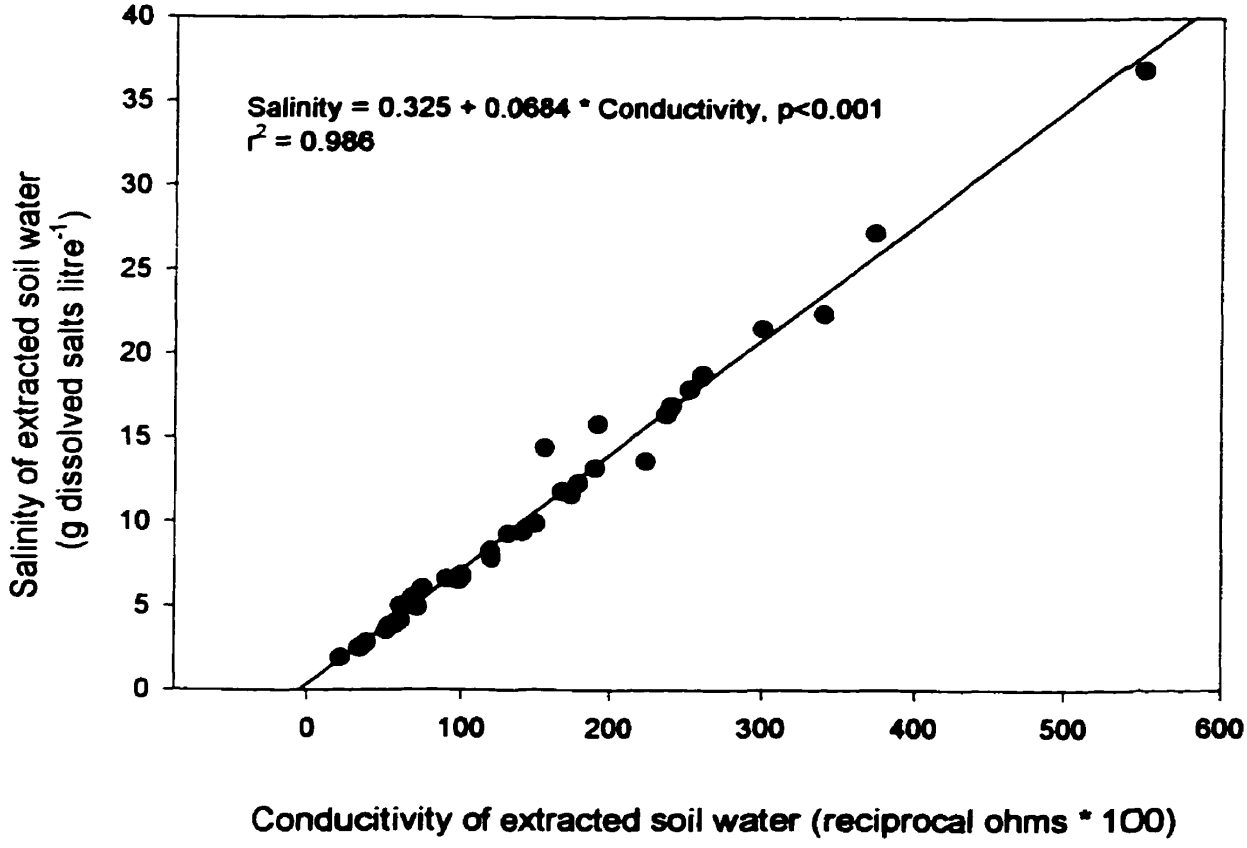


Figure 20. Simple linear regression of soil salinity (g dissolved salts litre^{-1}) using conductivity of extracted soil water (reciprocal ohms*100) as the predictor variable

Figure 21. Salinity of extracted soil water (g dissolved salts litre^{-1}) from high and low biomass swards of *Puccinellia-Carex*, bare ground and swards of *Festuca-Calamagrostis* from June to August, 1994. Black symbols represent soil samples taken from the field and grey symbols represent soil samples that had been watered twice a day with river water from early June to early August.

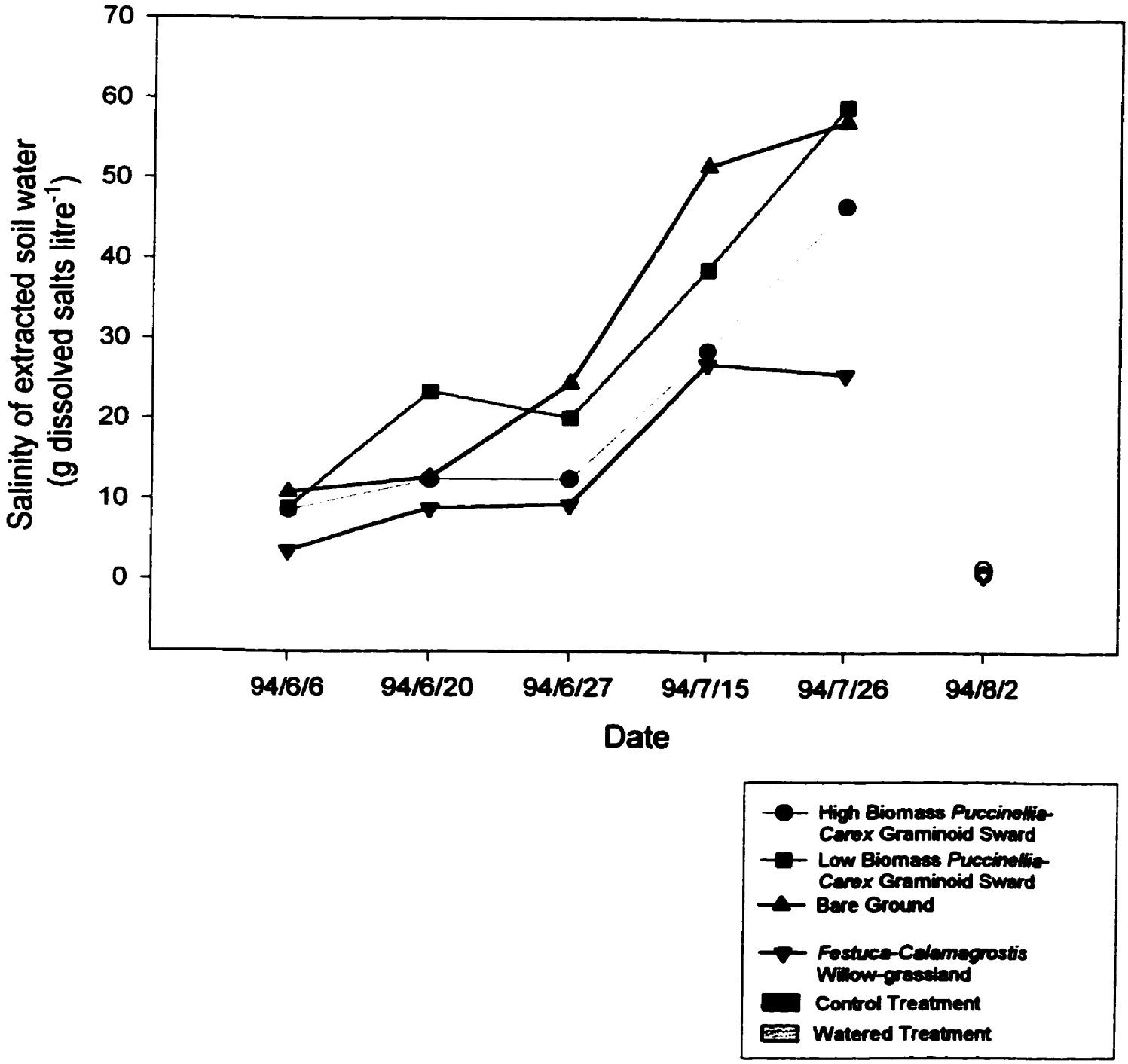

70
60
50
40
30
20
10
0
Salinity of extracted soil water
(g dissolved salts litre-1)
94/6/6
94/6/20
94/6/27
94/7/15
94/7/26
94/8/2
Date
High Biomass Puccinellia-Carex Graminoid Sward
Low Biomass Puccinellia-Carex Graminoid Sward
Bare Ground
Festuca-Calamagrostis Willow-grassland
Control Treatment
Watered Treatment

Figure 22. Standing crop measurements (g of dry mass m^{-2} ± standard error) of samples that had been watered twice a day with river water and samples that were left under field condition. Samples were sorted as (a) graminoids, (b) *P. egedii*, (c) *P. maritima*, (d) *S. borealis* and (e) *Salix* spp. The samples originated from four sites each of high and low biomass swards of *Puccinellia-Carex*, bare ground and swards of *Festuca-Calamagrostis*. A to C refer to Tukey-Kramer multiple comparisons of vegetation types that the pots were taken from; a to c refer to Tukey-Kramer multiple comparisons of sites in the bare ground assemblage; d to e refer to Tukey-Kramer multiple comparisons of sites in swards of *Festuca-Calamagrostis*.

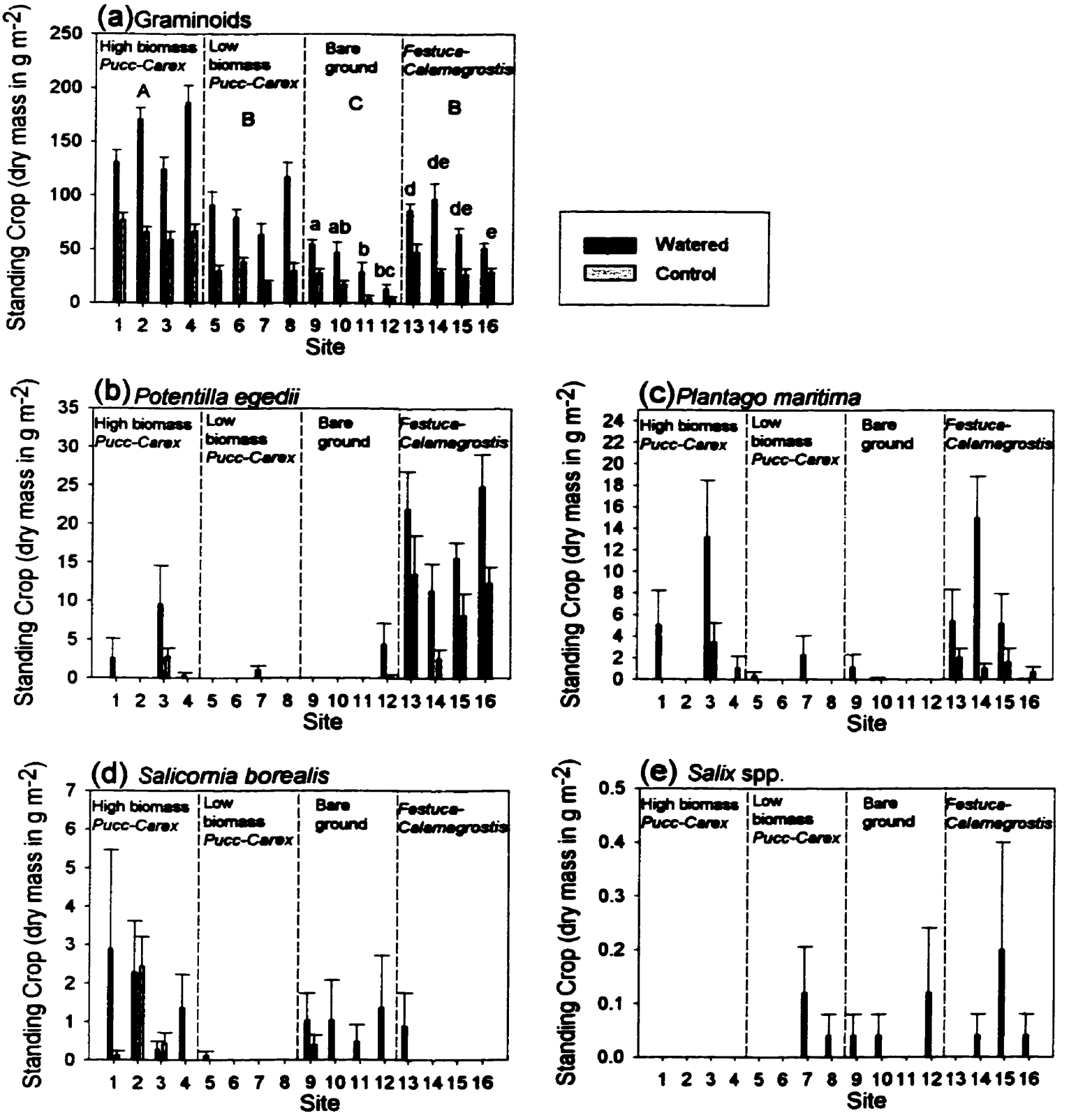
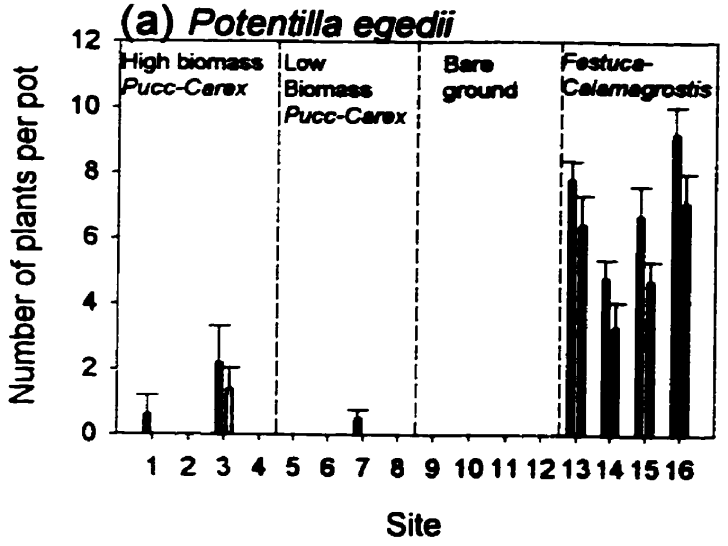
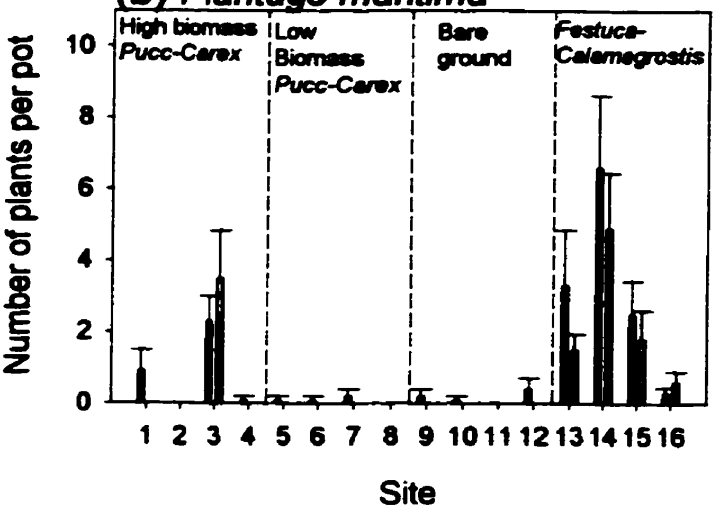
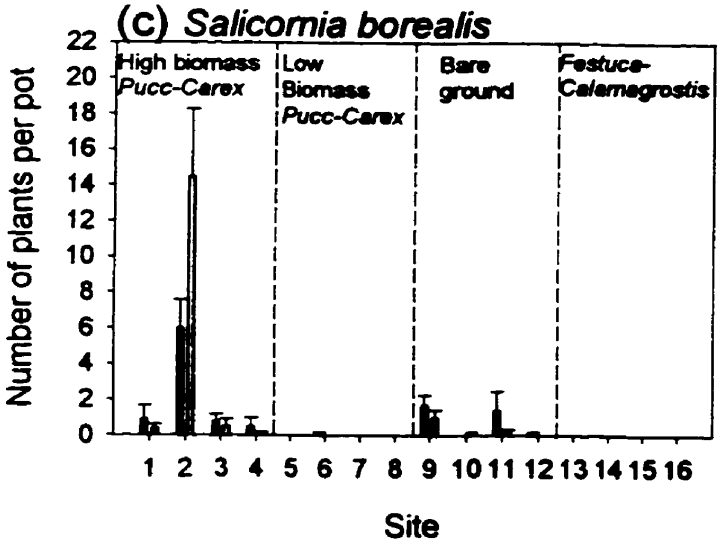
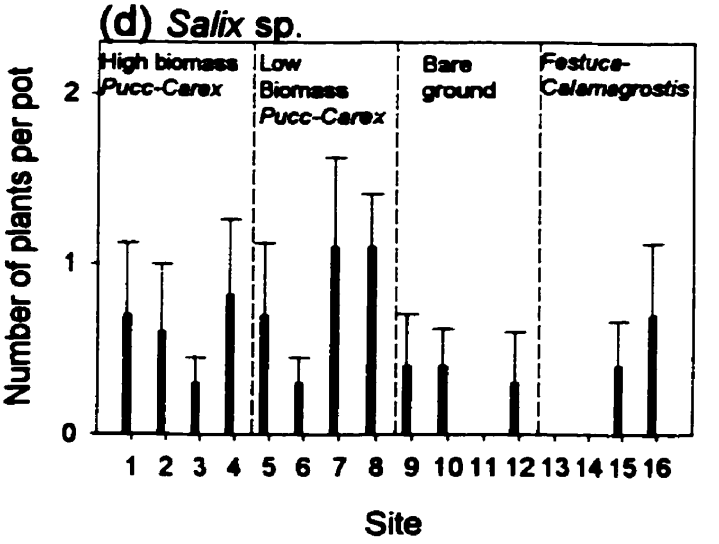

(a) Graminoids
(b) Potentilla egedii
(c) Plantago maritima
(d) Salicornia borealis
(e) Salix spp.
Standing Crop (dry mass in g m-2)
Site
High biomass Pucc-Carex
Low biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
A
B
C
B
a
ab
b
bc
d
de
de
e
Watered
Control

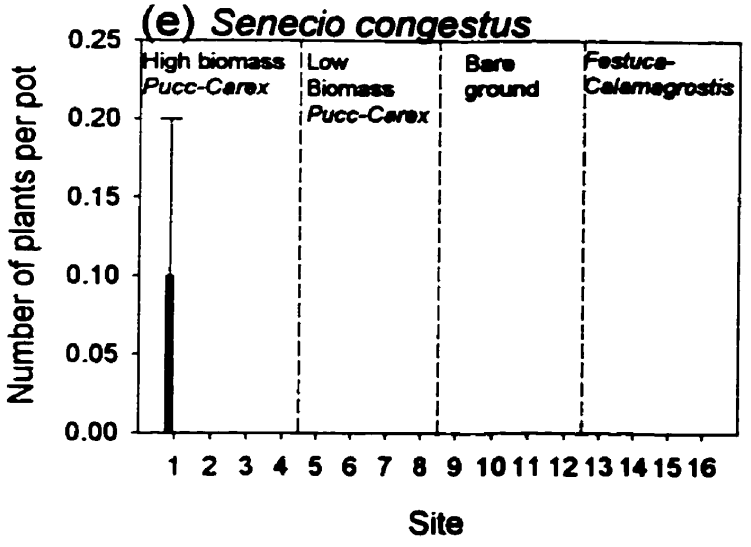
Figure 23. Average number of plants that were counted in flower pots that had been watered twice a day with river water and samples that were left under field condition on 27 July and 1 August, 1994 respectively. Samples were sorted as (a) graminoids, (b) *P. egedii*, (c) *P. maritima*, (d) *S. borealis* and (e) *Salix* spp. The samples originated from four sites each of high and low biomass swards of *Puccinellia-Carex*, bare ground and swards of *Festuca-Calamagrostis*.

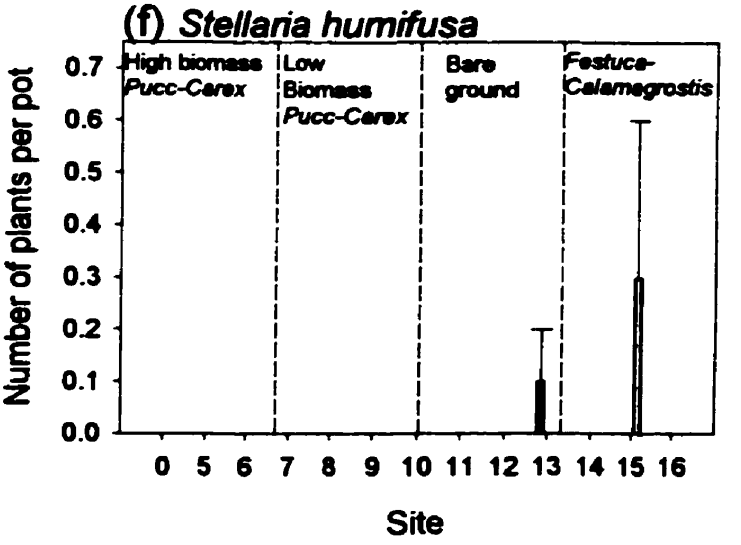

(a) Potentilla egedii
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site


(b) Plantago maritima
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site


(c) Salicornia borealis
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site


(d) Salix sp.
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site


(e) Senecio congestus
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site


(f) Stellaria humifusa
High biomass Pucc-Carex
Low Biomass Pucc-Carex
Bare ground
Festuca-Calamagrostis
Number of plants per pot
Site

were present in highest numbers in pots that originated from *Puccinellia-Carex* swards with a high biomass and from the *Festuca-Calamagrostis* swards. Seedlings of *S. borealis* were present in both the high biomass swards of *Puccinellia-Carex* and in bare soils but were almost absent from the swards of *Puccinellia-Carex* with a low biomass. Both seedlings of *Senecio congestus* and *Stellaria humifusa* were present in very low numbers in pots (Fig. 23e, f). For the dicotyledonous species, all recorded plants of *S. borealis*, *Salix* spp. and *S. congestus* were seedlings. Data for *P. egedii* and *P. maritima* were confounded and included resprouting of plants from underground organs and seedlings. However, when 100 plants of these species were haphazardly collected from the same sampling area the following year (1995), 13% of collected plants of *P. egedii* plants and 32% of plants of *P. maritima* plants were seedlings.

4.4 Discussion

4.4.1 Seed rain

Although the input of seeds in the seed rain was low during the growing season, there were no systematic differences between the seed rain at undamaged sites and sites where loss of vegetation and soil degradation had occurred. Much of this may be due to the apparently high dispersability of the seeds of some species and the open habitat in degraded areas. Some of the most common species found in seed rain of the growing season are dispersed by wind (e.g. *Salix* spp., *S. congestus*). Due to the open habitat at degraded areas, seeds can continue dispersing until a barrier or crevice is reached where seeds accumulate in sheltered microhabitats (Smith & Kadlec 1983, Chambers & MacMahon 1994, Inglis 1999) such as intact vegetation or seed traps. The numbers of

seeds trapped in disturbed sites were much higher than would be predicted by local production suggesting less retention of seeds and greater mobility in these areas. The seed traps are one of the few barriers present at these sites as the crusted algal mats and the dried, compacted soil on the surface (Chambers & MacMahon 1994) tend to preclude entrapment.

Similar processes are likely to affect dispersal during spring melt on a larger scale. The relative abundance of fresh-water species in the seed rain, which are dispersed over distances on the scale of kilometres, was much greater at spring melt than during the growing season. Flooding extended the dispersal range of species in two riparian sites in south-eastern central Sweden (Skoglund 1990). At La Pérouse Bay, the dominant species in the seed rain (*S. borealis*) together with a common fresh-water species (*Potentilla palustris*), are well adapted to dispersal by water. *S. borealis* floats by retaining air between the short flat hairs covering the testa and the floral bracts that often remain attached to the seed (Ungar 1978) and seeds of P. palustris have been known to float for months to years at a time (Skoglund 1990).

Seeds dispersed by water during spring melt will most likely have one of three fates: seeds may be trapped by intact vegetation, seeds may be washed into the bottoms of the many ephemeral ponds as the waters recede or seeds may be swept along ephemeral streams towards the Mast River and be carried away from the locality. In addition to dispersing seeds produced during the former summer and autumn, the floods during spring melt may redisperse seeds accumulated in the soil as the strong flood current causes soil erosion. Seed banks are often much more dynamic than they are portrayed to be (Chambers & MacMahon 1994).

The seed traps made of artificial lawn material were better mimics of intact graminoid swards than of bare soil in recreating the entrapment properties. In degraded soils, the number of seeds caught in traps represented seeds moving through the plot rather than seeds that would remain in the plot (actual seed input). A seed trap that was a better mimic of the texture of soil would provide a better estimate of the seed input, which could be compared to the number of seeds moving through the area.

4.4.2 Seed germination

Seeds of most halophyte species germinate in the spring or during the season of high precipitation when salt salinity is lower (Ungar 1978, Keiffer & Ungar 1997). Germination of seeds was severely impaired for three of the eleven species tested and non existent for seven others when the salinity reached 20% of that of oceanic sea water (~6.7 g of solute per litre). Soil water salinity was already higher than this value in soil of swards of *Puccinellia-Carex* swards by 6 June, 1994 and even soil from the *Festuca–Calamagrostis* swards exceeded this value by 20 June, 1994 (Fig. 21). These dates are very early in the growing season at La Pérouse Bay. No seeds germinated in the solution 60% the salinity of ocean seawater and this salinity was reached in soils from low biomass swards of *Puccinellia-Carex* and at bare ground sites by 27 June, 1994. Salinity inhibits germination as a result of both osmotic stress and specific ion toxicity (Ungar 1978, Ungar 1982, Woodell 1985). Some extremely salt-tolerant species are reputed to show "salt-stimulation" where germination is enhanced when seeds are exposed to hypersalinity and then placed back in distilled water (Woodell 1985, Keiffer & Ungar 1997). Unfortunately, only one seed of *S. borealis* germinated during the assay (in 5%

salinity of seawater solution). The low rates of germination of all species in deionized water or solutions of low salinity may be viewed as a type of bet-hedging in a highly unpredictable environment where salinity may increase rapidly in spring. This assertion assumes that the remaining seeds retain their viability over time. An alternative hypothesis is that the cold and freeze-thaw treatments may be inadequate to break dormancy and this accounts for the low rates of germination.

4.4.3 Establishment

Whether or not lowering the salinity results in increased establishment also depends on the assemblage of seeds in the soil at a site. For example, watering had the greatest effect on the number and biomass of both *P. egedii* and *P. maritima* plants in higher biomass sites where seeds were most likely to be trapped by the vegetation. Amelioration of soil conditions will have no effect if propagules are not present at a site as demonstrated by the lack of growth in low biomass and bare ground sites. However, high biomass sites can also provide much competition for seedlings as they establish.

Seed/seedling conflicts can account for the patchy response of dicotyledonous plants to the watering treatment compared to that of graminoids, which spread chiefly through vegetative mechanisms. Microsites favourable to seed trapping, retention and survival may not be favourable to seedling establishment and vice-versa (Schupp 1995, Chambers 1995a). The high biomass sites where seeds were more to be found were also sites with strong competition from established vegetation. The dominant graminoids were responding to a change in an environmental factor, whereas both dispersal and

changes in microhabitat conditions shaped the establishment patterns of dicotyledonous seedlings.

Irrespective of the magnitude of biotic interactions on seed germination and establishment, even moderate salinities are an effective constraint on these processes. Aqueous solutions may represent much more demanding conditions than soil systems where the adverse effects of salt may be alleviated by the presence of organic material.

Chapter Five: General Discussion

5.1 Responses of vegetation and soil seed bank to disturbance and stress as a function of the life history of plants

Foraging by lesser snow geese and accompanying changes in edaphic factors exert strong influences on the pattern and structure of plant communities at La Pérouse Bay by influencing gradients of disturbance and stress on plants (Chapter Three). In salt marshes, the loss of intertidal and supratidal graminoid swards and the associated dicotyledonous species, and the shift towards patches of salt-tolerant annuals and bare ground are reflected in the size and composition of the soil seed bank. Likewise, on beach ridges, loss of the dominant sand-binding grass, *Leymus mollis*, is associated in this habitat with increases in assemblages of "weedy" species, particularly *Matricaria ambigua* (Table 9). However, many of the ruderal species found in undamaged sites are also present in degraded sites. As the large seeds of *L. mollis* (Fig. 6) do not appear to contribute to the seed bank (Table 14), the seed bank of damaged plots are similar to those of undamaged plots (Fig. 16). The degree and patterns of change in both types of habitat can be related to the life-history strategies of the species found in both former and present-day communities.

Stress-tolerant species tend to be long-lived plants that spread through clonal growth (Grime 1979). At La Pérouse Bay, salt-marsh vegetation is exposed to stress arising from low temperatures, short growing seasons and saline soils. The undamaged salt marsh is composed mostly of perennial vegetation. The species with the highest cover frequencies, *Carex subspathacea, Puccinellia phryganodes, Potentilla egedii* and

Stellaria humifusa (Tables 5-9), are all salt-tolerant plants capable of extensive stoloniferous or rhizomatous clonal growth. In addition to tillering, *Puccinellia phryganodes* and *Carex subspathacea* can disperse and establish from plant fragments including individual leaves, shoot systems and tillers (Chou *et al.* 1992). In a study conducted in salt marshes located on the Gower Peninsula, South Wales (Ungar & Woodell 1996), the vegetation was similarly dominated by *Puccinellia maritima*, which did not form a persistent seed bank.

The most common species found in the soil seed bank at sites where the vegetation is undamaged are *Ranunculus cymbalaria*, *Hippuris* spp. and *Potentilla egedii* (Tables 10-14). Seeds of *Juncus bufonius*, an annual rush, were present in high densities at some plots but the distribution was very patchy. These species, with the exception of *P. egedii*, are not very common plants in the vegetation. Of these species, only *R. cymbalaria* (up to 9380 seeds m^{-2}) and *Hippuris* spp. (up to 1160 seeds m^{-2}) were present in substantial densities and found in all zones and at all depths of the salt marsh, although they were present at very low frequencies in the vegetation. Therefore, species that are characteristic of the undamaged salt marsh spread chiefly through clonal growth and do not substantially contribute to the soil seed bank, with the exception of *R. cymbalaria*. *R. cymbalaria* is present at low frequencies in the vegetation but dominates the seed bank. At a salt marsh near Churchill, Staniforth *et al.* (1998) found very high numbers of *Juncus bufonius* and *Spergularia marina* in the soil. These two species formed 92% of the total seed bank, which had a mean of 39,204 seeds m^{-2}. The difference in the seed-bank composition from the salt marshes at La Pérouse Bay can be attributed to the sandier soils and lower salinity (average of 10g of solute per litre; Griller & Lajzerowicz,

unpublished data). The salt marsh at Bird Cove is constantly inundated with tidal water and fresh water from streams (Staniforth *et al.* 1998). *J. bufonius*, a species commonly found with a large, persistent seed bank (Thompson *et al.* 1997) is usually found in disturbed but still undamaged swards rather than on hypersaline mud flats. *Spergularia marina* was found in small numbers in the soil of intertidal, supratidal and inland salt marshes at La Pérouse Bay. However, seed germination of *S. marina* is more inhibited by high salinity than *Salicornia europaea* (Ungar 1962, Keiffer & Ungar 1997), which is very closely related to *S. borealis*.

Abiotic factors, such as salinity, wave action and frequent tidal inundation, are thought to limit plant distribution in the seaward end of marshes (Bertness 1991a, b). The initial colonizer of bare sediments of emerging tidal flats is *P. phryganodes* (from plant fragments) followed by *C. subspathacea* (Jefferies *et al.* 1979, Handa 1998). Less tolerant of salt than *P. phryganodes* (Srivastava & Jefferies 1995b), the presence of *C. subspathacea* early in the colonization process is dependent on the availability of fresh water or frequent inundation by brackish water. In the deltas of the Mast River and Wawao Creek, *Hippuris tetraphylla* is the initial colonizer of unconsolidated sediments (Jefferies *et al.* 1979). Possessing a heterophyllous leaf, *H. tetraphylla* is able to survive under sustained inundation and is never found in dry areas not subject to tidal inundation or flooding from streams. In addition to clonal growth and propagation from severed rhizomes, it may also spread as a result of sexual reproduction as seed production is plentiful (E. Chang, personal observation). However, this species is less tolerant of salt than the other common species found in the salt-marsh vegetation and the seed bank. Salinity and desiccation may limit its seed viability and ability of seeds to germinate.

The colonizers of the salt marsh can be categorized as stress-tolerators on account of the build up of salinity and the drying out of soils in summer (*sensu* Grime 1977). Clonal propagation is a common regeneration strategy associated with stress-tolerators as vegetative offspring still attached and sustained by the parent plant suffer low mortality rates (Grime 1979).

P. phryganodes and *C. subspathacea* are capable of surviving under moderate rates of disturbance as they regenerate easily from plant fragments (Chou *et al.* 1992). Grazing of the *Festuca-Calamagrostis* assemblage in the supratidal marsh can lead retrogressively to *Puccinellia-Carex* swards (Hik *et al.* 1992, Handa 1998). When geese crop plants, they may facilitate spread by dispersing plant fragments and opening up suitable patches in the intact swards (Chou *et al.* 1992). However, these two species may be sensitive to sustained heavy grazing over a large geographic scale because of the absence of seed production in the case of *Puccinellia phryganodes* and the lack of sufficient seed production in *Carex subspathacea*. In addition, *Festuca rubra* and *Calamagrostis deschampsiodes* do not spread extensively by clonal growth. Due to the overwhelming numbers of geese, a plant survival strategy of escape in time is needed, rather than just an escape in space. *H. tetraphylla* and *R. cymbalaria* produce sufficient seed and they have been found in soils in disturbed habitats around La Pérouse Bay Field Station (E. Chang, personal observation). It is interesting to note that *Stellaria humifusa* was not found in the seed bank but its more ruderal relative, *S. longipes*, was common even though the two species have very similar vegetative growth and seed morphologies (Chapter Two).

Patches of *Salicornia borealis* and bare ground replace the former plant assemblages in the damaged salt marshes of the intertidal, supratidal and inland zone. Due to the extremely high soil salinity (up to 120 grams of solute per litre) (Iacobelli & Jefferies 1991) in these areas late in the growing season and the high rates of soil erosion, these salt-tolerant plants dominate both the above-ground vegetation and the seed bank below ground (Tables 5-8, 10-13). This species is at the limit of its distribution in northern coastal sites in Canada (Wolff & Jefferies 1987a, b) and its strategy may be viewed as being risky as it is an annual plant with an annual seed bank. However, the levels of disturbance and environmental stress are sufficiently high to select strongly for this stress-tolerant ruderal at the exclusion of almost all other plants. Similar to the case at La Pérouse Bay, 100% of the seed bank in a heavily grazed salt marsh was composed of two salt-tolerant ruderal species, *Salicornia europeae* (a close relative of *S. borealis*) and *Suaeda maritima* in South Wales (Ungar & Woodell 1996).

Ruderals tend to be short-lived species that spread through sexual reproduction (Grime 1979). Regeneration strategies include seasonal colonization of gaps, the dispersal of numerous, widely-dispersed seeds and persistence in the soil. As mentioned above, most of the vegetation on the beach-ridge sites is composed of ruderals with the exception of *Leymus mollis*. The greater physical abrasion from wind, wave and ice action combined with the less stable, sandy substrate produced a more disturbed habitat than that of the salt marsh before the arrival of the lesser snow goose colony in the mid-1950's (Cooke *et al.* 1995). This explains the high relative abundance of ruderals in the vegetation. The species common to both the vegetation and the seed bank are *Matricaria ambigua, Stellaria longipes, Ranunculus cymbalaria, Atriplex patula* and *Spergularia*

marina. *R. cymbalaria* had the highest relative abundance in the vegetation on the beach ridge followed by the exclosures in the intertidal marsh on the western coast of the Bay and the inland marsh. It is a species with wide ecological amplitude and its presence in the seed bank is ubiquitous.

Possessing a pappus, *S. congestus* is a widely dispersed biennial plant (Chapter Four). Common in disturbed sites, it can tolerate at least intermediate levels of salinity. The distribution of *Senecio congestus* seeds was probably due to the entrapment and retention properties of the sites. Although it was found most frequently in the vegetation of degraded intertidal sites on the western coast of La Pérouse Bay, its highest density in the soil was under undamaged plots on the western coast of the Bay and under beach-ridge plots. The dense vegetation of the exclosures on the western coast of the Bay and on undamaged beach-ridge sites, and the larger particle size of the sandy soils on the beach ridge help to trap and retain these larger seeds (Fig. 6). The accumulation of seeds in the sandy, beach-ridge soils, in general, was facilitated by the larger particle size as this allows for entrapment of larger seeds (Chambers 1995b) and greater ease in vertical movement down the soil column (Chambers & MacMahon 1994). *Senecio congestus* was also common in both soils of a disturbed sand bar and salt marsh near Churchill (Staniforth *et al.* 1998).

Similar shifts in species composition from long-lived, stress-tolerant species that propagate through vegetative mechanisms to short-lived, ruderal species that form seed banks as a response to disturbance have been shown in salt marshes (Hopkins & Parker 1984, Ungar & Woodell 1996), subarctic coastal habitats (Staniforth *et al.* 1998) and arctic and alpine systems (Freedman *et al.* 1982, Chambers 1993).

5.2 Constraints imposed by disturbance and stress on the seed bank dynamics

Constraints on seed bank and vegetation processes in the supratidal salt marsh, that are linked to grubbing and grazing by larger numbers of lesser snow geese and accompanying changes in the soil, will be discussed using the model of seed bank and vegetation dynamics shown in the introduction (Fig. 24). These constraints can occur at every life-history stage from growth of the plant and production of seeds to recruitment of seedlings back into the vegetation. In degraded systems, the rates of disturbance and stress character of "gaps" are so severe that the range of viable strategies utilized in such an environment available to plants are severely curtailed. The number of successful "regeneration niches" decreases steeply as very few species can produce viable seeds, disperse those seeds, have those seeds germinate and establish successfully under the environmental conditions.

(A) Vegetative propagation

The local extinction of vegetation caused by combined high disturbance and high stress precludes the possibility of local vegetative propagation. Even before the onset of vegetation loss and soil degradation, grazing by lesser snow geese decreased the number of stolons produced by *Ranunculus cymbalaria* and number of ramets produced by *R. cymbalaria* and *Potentilla egedii* (Sadul 1987). In addition, growth of axillary shoots or attached tillers for the two dominant species, *Puccinellia phryganodes* and *Carex subspathacea*, decreased in response to increased salinity before the growth of main shoots (Srivastava & Jefferies 1995b). Axillary shoots and attached tillers may serve

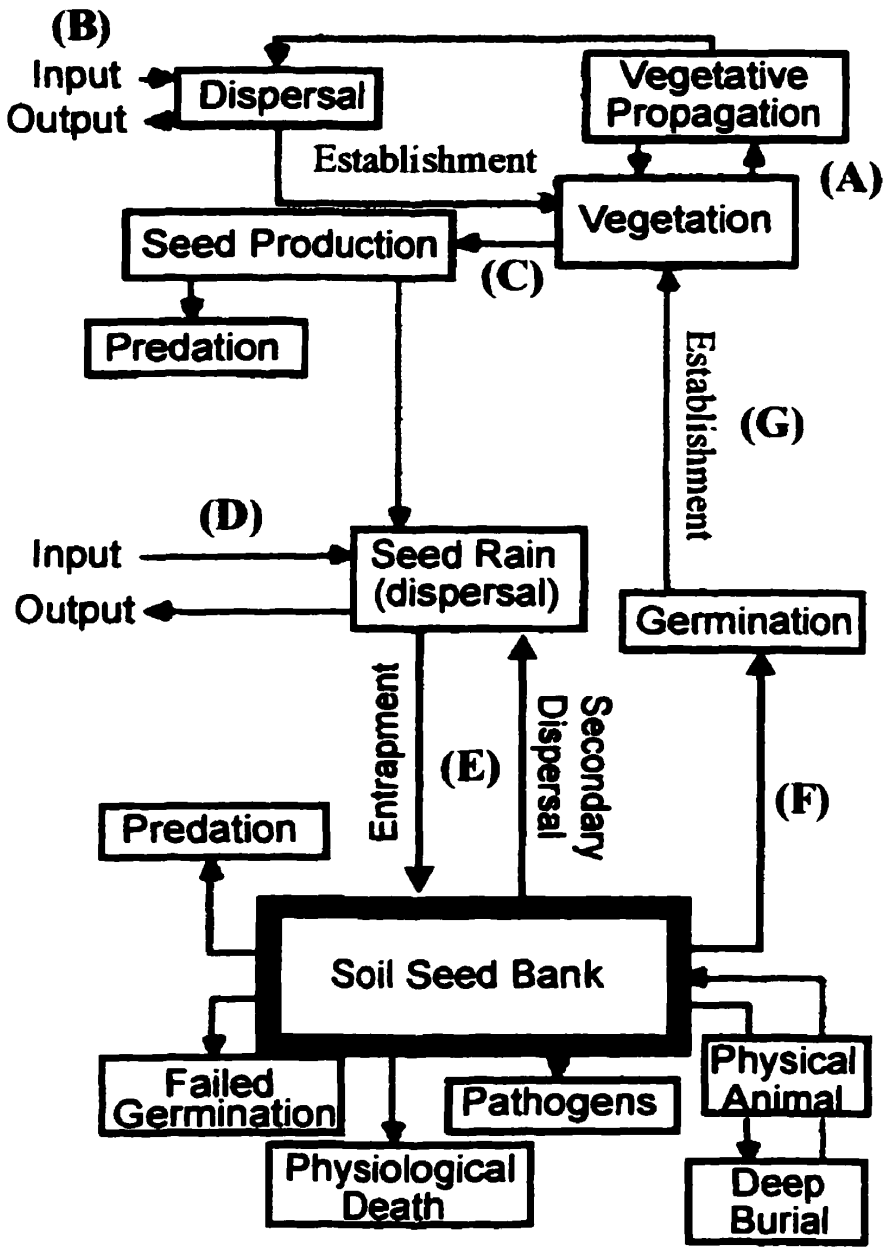


Figure 24. General model of seed bank and vegetation dynamics. A to F refer to stages that will be further discussed in the text. Modified from Simpson *et al.* (1989).

nonessential functions, such as expansion of a clone or dispersal of vegetative propagules, and as such, they may be inhibited before the death of the plant.

(B) Input of vegetative dispersal units

The dispersal range of clonal propagule units is generally more limited than that which is possible from seed dispersal as many vegetative (clonal) offspring remain attached to the parent plant and plant fragments do not survive for long in the absence of suitable habitat. The fragments do not have the ability to withstand or escape in time from stressful conditions unlike many seeds. Although grazing by geese can facilitate dispersal of fragments (Chou *et al.* 1992), the conditions of establishment are very poor in highly degraded sites. In inland marshes, revegetation of *C. subspathacea* was not observed in exclosures set up in 1984, except under the exclosure wire where litter had accumulated. In experimental studies ,which involved soil amelioration, success of *C. subspathacea* transplants was very low because of poor edaphic conditions (Handa 1998). In contrast, vegetation has established in all eight exclosures set up on the tidal flats in brackish locations on the western shore of La Pérouse Bay in 1992. In addition, assisted revegetation trials resulted in the establishment of complete swards of *P. phryganodes* within two years in some exclosures, although the success of revegetation was highly patchy (Handa 1998) reflecting the marked spatial heterogeneity of edaphic conditions at the microscale (<1 m^2).

(C) Seed production, predation and local seed rain

Sustained grazing may have a detrimental effect on seed production as flowering and fruiting are much higher in sites protected from herbivore grazing for most species (geese; Bazely & Jefferies 1986, musk oxen; Mulder & Harmsen 1995). Geese at La Pérouse Bay have been observed to eat seed heads of *Potentilla egedii*, *Plantago juncoides*, *Leymus mollis*, *Hippuris tetraphylla* and *Potamogeton filiformis*. Lack of predation may also explain the greater survival of seeds of *Ranunculus cymbalaria* in the soil compared with other species, as most buttercups are poisonous. Other predators that have been observed consuming seeds at La Pérouse Bay include passerines and shorebirds (Vacek 1999). Seed fragments of *Potentilla egedii*, similar to those retrieved from the soil while sampling for the seed bank, were found at a site where a granivore, most likely a passerine, had been feeding in 1998 (E. Chang, personal observation). As the density of these seed fragments was far greater than the density of viable seeds found in the soil, regeneration from seed by *P. egedii* may be detrimentally affected by seed predators.

Predispersal granivory has been shown to decrease seed pool in numerous studies (Bertness *et al.* 1987, Kjellsson 1985, Klinkhamer & de Jong 1989, Schupp 1988, Greig 1993, Windus & Snow 1993, Sperens 1997). However, whether granivores actually limit plant establishment is increasingly debated (Andersen 1989, Crawley 1989, 1990, 1992, Louda 1994, Louda & Potvin 1995, Maron & Simms 1997). If plant populations are limited by "safe sites" rather than seed availability, seedling recruitment is constrained by the number of suitable microsites rather than seed density and the effect of seed

consumers on plant populations would be minimal. However, see discussion on this issue in Chapter Four.

(D) Immigration of seeds

In the supratidal salt marsh at La Pérouse Bay, the vegetation and the seed bank were generally more similar in composition than the vegetation and the seed rain. The high dispersability of some species, due to wind or water, brought in the seeds of species not present locally in the above ground vegetation (e.g. *Betula glandulosa, Myrica gale, Saxifraga hirculus, Hippuris* spp., *Carex aquatilis, Potamogeton filiformis,* and *Potentilla palustris*). However, there were no systematic differences in seed composition between the seed rain collected in undamaged and degraded sites (Chapter Four). Many of the species immigrating to the site were either fresh-water species that would not establish in the salt marsh (e.g. *Betula glandulosa, Myrica gale, Carex aquatilis, Potamogeton filiformis*) or ruderal species indicative of degradation (e.g. *Senecio congestus, Salicornia borealis*).

Long-distance transport of seeds by wind or water (tides; Huiskes *et al.* 1995, flooded river water; Skoglund 1990) has been demonstrated in many studies (Howe and Smallwood 1982, van der Pijl 1982, Murray 1986). However, as in the previous section, the importance of dispersal in regulating patterns of plant distribution must be assessed in relation to the availability of "safe sites" and stage-specific mortality of plants (Houle 1995). After seeds are dispersed to a site, the actual recruitment of plants is regulated by a series of abiotic and biotic factors from the seed to adult stage (Houle 1996).

(E) Entrapment and retention of seeds

The texture of the soil surface and diaspore morphology have been shown to have a significant effect on the entrapment of seeds. A study conducted in a disturbed alpine system in Montana showed that the total number of seeds trapped and vertical movement in the soil column increased with increasing particle size until a threshold soil particle size was reached (Chambers *et al.* 1991). More numerous small seeds were trapped by small soil particle sizes than large particle sizes.

Vegetation patches have been shown to considerably enhance the entrapment of diaspores in windy, arid habitats (Nelson & Chew 1977), high-alpine sites (Chambers *et al.* 1991, Chambers 1995a, b, Urbanska 1994a, b, 1995a, b) and subarctic/arctic tundra (Urganska 1997a, b) (as reviewed by Urbanska 1997c). An interesting aspect of this "nurse" phenomenon in the Arctic is the widespread observation of crytograms in this function (Urbanska 1997c). The lack of a vegetation template, the compacted soil and the hardened algal crust restrict seed entrapment in areas with degraded soils at La Pérouse Bay. In addition, seeds on the surface of the soil or just beneath may be redispersed during spring melt (Chambers & MacMahon 1994) as the strong flood currents cause soil erosion.

(F) Germination of seeds

The germination of most species was inhibited by salinity around 6.7 g of dissolved solutes per litre, which is much lower than that commonly found in the edaphic conditions in the salt marsh. Seed germination of even halophytes is often depressed by exposure to high salinity (Ungar 1978, Woodell 1985, Keiffer & Ungar 1997). However,

halophytes differ from glycophytes in that they can recover once they are exposed to less saline conditions. Therefore, hypersalinity may not only act as a constraint at the germination stage *per se* but also differentially affect the survival of seeds in the soil. Observation in the field at La Pérouse Bay indicated that only salt-tolerant ruderals characteristic of degraded sites show high rates of germination in highly saline soils (e.g. *Salicornia borealis*).

(G) Establishment

Ameliorating habitat conditions by adding fresh river water to turfs did not always result in higher rates of establishment of seedlings. All the constraining processes prior to this stage act to decrease the success of seedling establishment. However, soil amelioration over a longer period of time than one growing season may result in greater success. Some exclosures that were set up on the tidal flats on the eastern shore of the Bay and planted with *P. phryganodes* in an organic mulch to which nutrients were added, spread rapidly and the new swards have been colonized by dicotyledonous species within two years (Handa 1998). Until recently, the role of dispersal processes in determining patterns in plant distribution and species richness have been largely ignored in favour of establishment conditions (van der Pijl 1982, Murray 1986, Fenner 1993). However, the dispersal of seeds may become limited in habitats increasingly fragmented through human land-use patterns (Poschlod & Bonn 1998). Degraded sites occur in moderate proximity to undamaged sites at La Pérouse Bay at present. As the scale of disturbance increases, revegetation will eventually become limited by seed availability.

5.3 Application of statistical methods to studies of seed banks

As noted before, the distribution of seeds in the soil is rarely normal. The highly skewed nature of the data and the high incidence of zero values preclude the use of transformations, even y=log(x+1). During the course of this study, I found generalized linear models (Crosbie & Hinch 1985) difficult to apply as the distribution of much of the data was unknown and was subsequently shown to deviate significantly from Poisson and negative binomial distributions. Unlike ANOVA, where tests can be conducted on the normality and homogeneity of variance of the data, it is difficult to rigorously test the suitability of a model and the underlying distribution. In many cases, nonparametric methods were used to test for main effects in lieu of generalized linear models.

5.4 The potential role of seed sources in revegetation at La Pérouse Bay

Handa's (1998) study of the potential for revegetation at La Pérouse Bay concluded that if goose populations were controlled, revegetation of the dominant graminoids was possible in younger, intertidal marshes as long as sources of dispersules remained, but would be extremely difficult in older marshes where vegetation had been absent for a number of years. Once a graminoid template can be established, revegetation from the relict seed bank of former salt-marsh plants in the more recently degraded areas (intertidal plots on the west coast of the Bay, some supratidal plots) is possible. Due to the open habitat and wind and water movement, seeds of some species are also capable of dispersal on the scale of kilometers. Sites on the eastern coast of the Bay may receive seed from tidal inundation and from the fringe of willow shrubs to the east. However, establishment conditions may be too poor in this area to support revegetation without

amelioration of soil conditions. Mulching, in addition to lowering salinity and retaining water can also help in trapping and retaining seeds and plant fragments (Chambers & MacMahon 1994). Obtaining, applying and anchoring mulch on such a large scale would be very expensive and laborious.

In accordance with Handa's study, revegetation from seed sources in the inland marshes would be unlikely. The loss of vegetation and soil degradation has occurred on such a large scale and for a long period of time that even exclosed areas with apparently high seed production do not accumulate seeds. The only species present in the seed bank in any quantity are *S. borealis* and *J. bufonius*, two opportunistic species. The *S. borealis* assemblage represents a "lost sere" as it does not accumulate sufficient litter and cannot facilitate colonization by other species at least over ecological time (<15 years). Each year, plant litter from stands of this annual is blown or washed away exposing the mineral substrate.

Many studies on the revegetation potential from natural seed sources have indicated that revegetation may be difficult. Limitations in revegetation potential posed by the dominance of the seed bank by "weedy" species in disturbed habitats as well as the transient or short-term persistent nature of seeds of target communities (i.e. communities present before disturbance) have been noted in grasslands (Kinucan & Smeins 1992, Bakker *et al.* 1996b, Hutchings & Booth 1996, Pywell *et al.* 1997, Bakker & Berendse 1999) and dry tropical ecosystems (Skoglund 1992). The "weedy" syndrome of seeds found in disturbed soils has also been found in arctic and alpine sites (Freedman *et al.* 1982, Chambers 1993) and wetlands (Wisheu & Keddy 1991,Ungar & Woodell 1996, Staniforth *et al.* 1998). In a review on European grasslands and heathlands, Bakker &

Berendse (1999) state that many species of interest in restoration projects are not present in the soil seed bank and have limited ranges of dispersal. This is not surprising as the high levels of stress and disturbance in degraded habitats select for the survival and persistence of species with ruderal or stress-tolerant ruderal life strategies. Regeneration through persistent seed banks and numerous, widely dispersed seeds is characteristic of ruderal species. In other words, if species possess persistent seed banks or widely dispersed seeds, we would not likely be faced with situations where their revegetation potential must be assessed.

In addition to ascertaining presence in the seed bank and seed rain, studies of revegetation potential must also consider the effect of abiotic factors on later stages in the life-history of plants (Houle 1995, 1996). Prins *et al.* (1998) developed a model to assess the feasibility of habitat restoration incorporating data on past and present distributions of plants and seeds, and probabilities of germination from the seed bank, dispersal and establishment. Their assessment concluded that 50% or even more of target plant species (species characteristic of former natural communities) would not appear in target areas (disturbed habitats) in the Netherlands within a period of 100 years. A regeneration index, developed by Bekker *et al.* (1997), showed that sites with a short history of abiotic change or biodiversity degradation are likely to be most worthwhile for restoration purposes.

Most species under threat of local extinction, as a consequence of human activities, do not have life strategies that incorporate long-term survival of seeds in the soil or sufficient dispersal of seeds over space. The probability of restoring these species from extant seed sources decreases with the passage of time and the practice of

introducing species to habits is currently under heated debate (van Groenendael *et al.* 1998). Revegetation of vast areas, such as the Hudson Bay lowlands, through introduction of species and intense management would be very difficult. As such, management practices should aim at reinstating suitable habitats for the establishment of species while regeneration from natural sources is still tenable.

Appendix 1. Character list for the DELTA database

Seed Shape Modifiers

#1. Wings or margin

1. present (must be persistent e.g. *Betula glandulosa*)

2. absent

#2. Style (beak) (short style is often referred to as a beak)

1. present (must be persistent e.g. *Triglochin maritimum*)

2. absent

#3. Bracts (bracts are modified leaves, not a part of the actual seed (small fruit) unlike margins or wings)

1. present (must be persistent e.g. *Myrica gale*)

2. absent

#4. Hairs (includes awns and pappuses)

1. short hairs present (less than a quarter of the seed length)

2. long hairs present (longer than half the length of the seed)

3. absent but indication of hair attachment (e.g. pappus rim)

4. absent

Seed Dimensions

#5. Length of seed (small fruit) (ENTER AS A RANGE; measured from base (hilum) to apex; includes persistent style, wings and bracts, excludes hairs and awns)

#6. Width of seed (small fruit) (ENTER AS A RANGE; measured greatest width 90 degrees to length, includes persistent wings and bracts, excludes hairs and awns)

Seed Shapes

#7. Planar seed (small fruit) shape (overall shape of seed excluding wings, style and hairs; base is positioned at the hilum)

1. elliptic
2. oblong
3. rhombic
4. ovate
5. obovate
6. triangular
7. obtriangular
8. oblique
9. irregular

#8. Cross-sectional seed (small fruit) shape

1. elliptic
2. oblong
3. rhombic
4. ovate
5. triangular
6. irregular
7. oblique

Seed Surface

#9. Network on seed (small fruit) surface

1. areolate (surface is smooth but marked with a network e.g. *Menyanthes trifoliata*)
2. reticulate (e.g. *Parnassia palustris*)
3. absent

#10. Elevations on seed (small fruit) surface

1. granulate (e.g. *Saxifraga caespitosa*)
2. tuberculate (wart-like projections e.g. *Carex consimilis*)
3. aculeate (prickly or spine-like projections)
4. pusticulate (low projection like a blister or pimple e.g. *Gentiana propinqua*)
5. colliculate (rounded or hillock-like elevations e.g. *Carex subspathacea*)
6. absent

#11. Lines on seed (small fruit) surface

1. lineate (marked by fine parallel lines e.g. *Hordeum jubatum*)
2. sulcate (furrowed or grooved e.g. *Ranunculus aquatilis*)
3. ribbed (e.g. *Senecio pauperculus*)
4. wrinkles
5. absent

#12. Orientation of lines on seed (small fruit) surface

1. longitudinal
2. transverse

#13. Porous texture to seed (small fruit) surface

1. present (e.g. *Arctostaphylos alpina*)
2. absent

Biogeography

#14. Geographical distribution <delimited by minimal distribution>

1. cosmopolitan
2. circumpolar
3. Amphi-Atlantic (occurring on both sides of the Atlantic Ocean but lacking on the Pacific side of the globe)
4. Amphi-Beringian (occurring on both sides of the Bering Strait but lacking on the Atlantic side of the globe)
5. North America (does not necessarily occur on entire continent)
6. Asia (does not necessarily occur on entire continent)
7. Europe (does not necessarily occur on entire continent)

#15. Geographical Distribution: North America

1. eastern
2. north-western
3. Western Hudson Bay
4. Mackenzie River delta

#16. Geographical Distribution: Europe

1. northern
2. north-western

#17. Geographical Distribution: Asia

1. eastern
2. north-eastern
3. eastern Siberia

#18. Eco-Region

1. arctic
2. high arctic
3. low arctic
4. sub-arctic
5. alpine
6. boreal
7. non-arctic

Soil Seed Bank Ecology

#19. Soil seed bank (1997, 1998 sampling in La Pérouse Bay salt marshes)

1. present
2. absent

#20. Growing season seed rain (1997, 1998 sampling at La Pérouse Bay salt marshes)

1. present
2. absent

#21. Spring melt seed rain (1997, 1998 sampling in La Pérouse Bay salt marshes)

1. present
2. absent

#22. Adult vegetation (1997, 1998 surveys in La Pérouse Bay salt marshes)

1. present

2. absent

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